

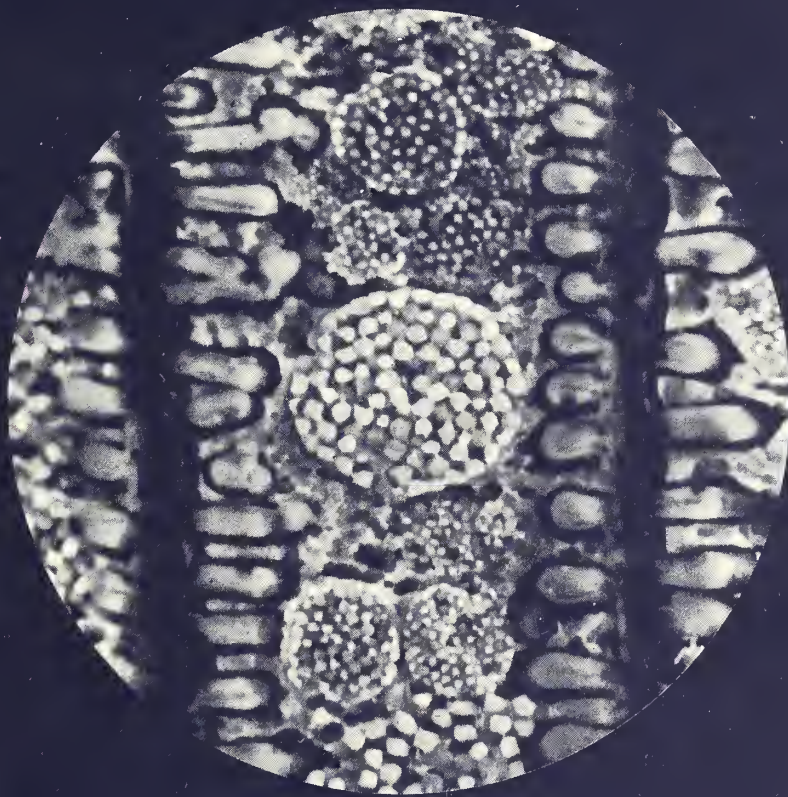




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Palaeontology

VOLUME 33 · PART 3 AUGUST 1990



Published by

The Palaeontological Association · London

Price £30

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THE CLASSIFICATION OF THE FORAMINIFERA – A REVIEW OF HISTORICAL AND PHILOSOPHICAL PERSPECTIVES

by JOHN R. HAYNES



ABSTRACT. A historical review of the classification of Foraminifera reveals that the latest by Loeblich and Tappan is in the central tradition, leading from the work of the early English School, in which it is attempted to relate test composition and fine structure to physiology in formulating a sound basis for distinction of suprageneric rank. Although the early English School first distinguished homologous from analogous structures, their view that Foraminifera constituted a primitive, plastic group has inhibited biological and stratigraphical work, and distorted classification down to the present. The search for a single 'key' to turn the problem has also led to swings of fashion and, using Brady's metaphor, to 'cutting rather than untying the Gordian Knot'. Recent classifications are shown to retain considerable artificial elements. Attempts to substitute numerical taxonomy or cladistics for 'intuitive' taxonomy are misguided. Principles to assist the way forward are given.

THE Foraminifera are the most abundant marine invertebrates and play a major role in the economy of nature. The classification given in the *Treatise of invertebrate paleontology* (Loeblich and Tappan (1964) hereafter referred to as *Treatise* (1964)) has been treated as a standard for a quarter of a century, so the appearance of a comprehensive revision in book form (Loeblich and Tappan 1988a) is a considerable scientific event, not only for palaeontology but also for zoology. Its importance for geology is well expressed by the authors in their introduction: 'They are the most widely used fossil organisms for biostratigraphy, age dating and correlation of sediments, and paleoenvironmental interpretation, both as organisms whose living representatives provide ecologic data and as mineralized shells that are a geochemical record of paleotemperatures, extent of glaciation and other paleogeographic features' (p. 1). However, the very success of Foraminifera in applied palaeontology and palaeoecology has hindered advances in classification because workers have resisted changes, preferring the 'stability' created, at least in the West, by general acceptance of the *Treatise*. Indeed, suggested changes may provoke hostility. Symptomatic of the general attitude is this complaint in *Nature* about the alternative classifications put forward in *Comparative primate biology* (Martin 1988, p. 589): 'The Editors did not impose a uniform system... use of alternative schemes seen as a sign of healthy science better seen as an insidious ailment... a relatively stable classification is a prerequisite for other work... it is high time matters were put to rights... the present situation is comparable to a team of computer programmers arguing endlessly about whether they should use BASIC, FORTRAN or PASCAL, rather than getting on with the actual programming job in hand'.

Views of this kind mistake the fundamental purpose of classification which is to provide an orderly hierarchical array of taxa reflecting the genetic lines of descent, not simply to provide a convenient pigeon-holing, i.e. a natural classification is confused with an artificial identification key or retrieval system. A taxonomic scheme is useful for 'other work' in direct proportion to the extent it reflects the true lines of descent. An artificial scheme will probably be misleading in biostratigraphy and palaeoecology and certainly useless for studies of macro-evolution. It is the advances towards a genetic classification that are a prerequisite of greater precision in other work, especially in study of rates of evolution and diversity patterns. A good example is provided by the foraminiferal genera

Globigerina and *Globorotalia*, formerly included in one family and both considered to range back into the early Cretaceous. In Loeblich and Tappan's book they are now placed in different superfamilies and both are restricted to the Cenozoic, *Globorotalia* to the Neogene. The discovery that the globigerinids are near-surface plankton while the globorotaliids are deep-dwellers is in tune with this more discriminating approach. Similarly, the large orbitoidal foraminifera were originally placed in one family that straddled the Cretaceous-Tertiary boundary. Again, these genera are now recognized as belonging to distinct superfamilies with ranges which reveal and emphasize the marked break at that horizon. Changes of this kind are clearly a sign of scientific health and complaints about them reminiscent of the lamentations that arose because Copernicus destroyed the stability of the Ptolemaic system.

Another reason for the 'bad press' given to taxonomy is the common misconception that the important work on the major groups has been done, with the main goals achieved. Like the traditional comparative anatomy once taught at Oxford (as described by Sir Peter Medawar in his engaging autobiography, *Memoirs of a thinking radish*), it is seen as 'deadly dull' and no longer a 'live' issue, despite the 'grandeur' of the demonstration of evolution. Controversies in taxonomy are dismissed as mere squabbles about trivial matters, such as priority of names, and descriptive work on new species as a higher form of stamp collecting. However, there are very few groups in which the phylogeny is known with any certainty. In the Foraminifera it is a matter of continuing lively debate and a comparison between the classification set out by Loeblich and Tappan in their new book and those of earlier workers, including their own in the *Treatise* (1964), will silence criticism of this kind.

The general reader may be given a clearer picture of the problems faced in the attempt to produce a natural classification by a historical summary of past debates about the correct principles to be followed. The clash between the 'English School' and the 'Continental School' in the nineteenth century and between the English School and the 'American School' in the early twentieth century being particularly instructive, because the extreme positions taken up highlight the difficulties involved as well as differences in philosophy and attitude. This will also help to explain the paradox that late into this century the Foraminifera could be regarded as a simple, plastic group in which the shell composition reflected habitat, and differences in shape and ornament the impact of physico-chemical forces acting on the protoplasm (D'Arcy Thompson 1942), at the same time as they were being successfully used in biostratigraphy. No attempt is made to summarize all the classifications that have been proposed (for an exhaustive coverage see Loeblich and Tappan 1964, pp. 140-63). Instead, attention is directed to the most influential classifications in what may be called the central tradition; in particular, to the founder members of the English School because they were the first successfully to distinguish homologous from analogous structures and because the classification now produced by Loeblich and Tappan is, in many respects, 'the direct lineal descendant' of that of Carpenter (1861, 1862).

ATTEMPTS TO UNTIE THE GORDIAN KNOT

The clash between catastrophism and uniformitarianism

The dominant figures in the English School were largely biological in outlook and, appropriately for a maritime nation, were chiefly concerned with the study of the Recent and the dredge samples that became available as a result of the strong nineteenth century drive towards exploration of the oceans. The first work on foraminifera in England was on the Recent species of the south coast (Walker and Boys 1874). The dominant figures in the Continental School were largely palaeontological and geological in outlook, the first work in France being that on the Eocene of the Paris Basin (Lamarck 1804). There was also a deeper dichotomy in that Alcide d'Orbigny, the founding father of scientific foraminiferal studies and of the Continental School, was also a catastrophist (appropriate in post-revolutionary France), whereas, in contrast, the English School was strongly influenced by Lyellian uniformitarianism (see Heron-Allen 1917).

D'Orbigny (1826) was the first to recognize the Foraminifera as a separate group, considering them an order of the Cephalopoda distinguished by possession of a series of internal, basal chamber openings (foramina), rather than possessing a siphuncle. Concordant with his idea that the Foraminifera were cephalopods he divided them into families entirely on the basis of chamber arrangement or coiling mode, the simplest (and most severely parsimonious) solution.

After the discovery that Foraminifera were Protozoa by Dujardin (1835), d'Orbigny (1839) raised the group to Class status with six orders based on chamber arrangement, plus an extra one for single chambered forms. Despite the simplicity of his taxonomic scheme, d'Orbigny recognized a large number of genera and species. This was because he believed in the complete replacement of faunas at the end of each successive geological stage by special creation.

Although the discovery that the Foraminifera were Protozoa prompted d'Orbigny to give them class status, it had little other effect on his view of their classification. In contrast it had a profound influence on the whole philosophy of the English School, dominated by Williamson and Carpenter in the mid nineteenth century. Thus, Williamson (1858, p. ix) saw it as demonstrating the 'low organization' of 'diversified inferior creatures' with an 'anomalous and obscure' history. The external features of the shell, such as direction of growth and sculpture, considered important earlier when foraminifera were thought to be molluscs, were now seen as due to 'age and local circumstance' and possessing 'little value'. Carpenter (1862, p. vii) in classing them with the Rhizopoda commented on the soft parts as 'a little particle of homogeneous jelly', the 'protoplasm not yet differentiated into cell-wall and cell-contents' and more primitive than *Amoeba*, because, apparently, without nucleus. For this reason he concluded that variation in form of the shell aperture, which in higher animals with an alimentary canal would warrant generic or family distinction, was of 'comparatively little moment' and perhaps even a matter of 'individual difference'.

Both these key figures in the English School readily accepted the new doctrine of Darwinian evolution: Carpenter was close to the Darwin circle, wrote a supporting review (1860) and took a prominent part in debates on the subject as, 'one of the most active and respected interpreters of evolutionary theory' (Young 1985). Combined with their view of the low position of Foraminifera on the tree of life, this led them to reject outright d'Orbigny's classification based on geometrical plan. The 'extraordinary diversity' of Foraminifera and 'the gradational nature of these differences' which indicated 'community of descent more or less remote... from a small number of original types', also led them to dismiss not only his successive special creations but also his 'needlessly... multiplied... number of species'.

Williamson (1858, p. x) decided that 'real specific' features would only be shown by the soft parts, and that 'the hard shells of the Foraminifera do not constitute a sufficiently constant and important element in their organization to justify our trusting to them as guides in the discrimination of species'. While Carpenter (1862, p. vii) was forced to the conclusion that 'sharply defined divisions – whether between species, genera, families or orders do not exist' and that (p. x) the 'ordinary notion of species... was inapplicable', the term becoming one of convenience for intergrading assemblages grouped round a small number of family types, showing 'continuity through a vast succession of geological epochs'.

It would be anachronistic to complain that Carpenter and Williamson lacked an adequate species concept. The attempt to apply evolutionary ideas was premature. Adequate knowledge of the stratigraphical record, of true genetic diversity as distinct from dimorphism and polymorphism resulting from alternation of generations, and of the complications caused by changing apertural style during the growth of multiform species, lay in the future. But they were correct in their scathing attack on members of the Continental School, such as de Montfort (1808) who recognized individual variations as generic, e.g. nine genera based on '*Nautilus calcar*' – all synonymized with *Lenticulina* in Loeblich and Tappan's book. But in their extreme reaction to d'Orbigny on the side of Lyellian uniformitarianism they denied (Carpenter 1862, p. xi) there was 'any fundamental modification in the foraminiferous type from the Palaeozoic period to the present', and deduced (Williamson 1858, p. xii) that foraminifera have 'little value... in determining the relations between

zoological provinces or in identifying stratified deposits'. These views cast a long shadow down the years, inhibiting stratigraphical work in Britain into the present century, despite their countervailing (and contradictory) remarks on the value of foraminifera as indicators of temperature and depth. They undoubtedly influenced Darwin, who otherwise might have found a paradigm in these 'intergrading forms' regarded as the 'direct lineal descendants' of remote ancestors. On this subject the first edition of the 'Origin' preserves a resounding silence, and, significantly, Carpenter does not mention foraminifera in his extended review of it (1860). In later editions (from the 4th, 1866, p. 402, see 1929 reprint of 6th edition, p. 293) Darwin notes 'Foraminifera have not, as insisted by Dr. Carpenter, progressed in organisation since even the Laurentian epoch'. Even a hundred years later it was concluded 'the morphological series... do not always seem to have very strong claims to being evolutionary series' (Challinor 1959, p. 79).

The confusion about the value of the foraminifera in stratigraphy is a symptom of the confusion about species caused by the advent of Darwinism. When Carpenter (1862, p. x) states that the idea of the species as 'marked out from each other by definite characters... from original prototypes similarly distinguished', is quite inapplicable to this group, with the suggestion that this is unlike the case in the more advanced Cephalopoda, we see the persistence of the Linnaean idea of the species, i.e. separated by morphological gaps from their nearest relatives in the great chain of being. Underlined by his view (1860, p. 214) that the chief difficulties for Darwin's theory were those structures or habits 'difficult to imagine to have been acquired gradually by any process of consecutive modification'. Again echoed by Challinor (1959, p. 62), 'the apparent rarity of closely graded evolutionary series may express a real rarity and be due... to evolution usually proceeding in jumps rather than perfectly smooth gradation'. In this way, paradoxically, the profoundly anti-Darwinian, Linnaean species, the discrete 'particle' of Lyell, became incorporated into the philosophy of the English School as a justification of extreme lumping in the search for the 'morphological gap' between 'true' species. The pervasive influence of this idea, even today, is seen in ill-advised attempts to delineate this 'true' species by 'scientifically rigorous' methods, involving numerical taxonomy and cladistics (see p. 521).

Although the attempt to apply evolutionary ideas at the specific and generic level was a failure, the attempt to find a more natural basis for the higher divisions was much more successful. Both men (Williamson, a medical doctor and Professor of Natural History and Carpenter, one of the leading physiologists of his time) were highly skilled microscopists and their background and training prompted them to look for the possible connection between soft parts and fine structure and wall composition (texture) of the test, as a means of recognizing major groups. Carpenter (1850, 1856, 1862) made particular use of both natural and artificial casts as well as thin-sections in his studies of foraminifera from off Australia and the Philippines which included a number of larger calcareous genera. This led him to the discovery of canals and the distinction that could be drawn on the basis of the presence or absence of pores between annular discoid genera grouped together by d'Orbigny. By means of thin-sections and transmitted light, Williamson (1852, 1858) distinguished the three major wall structure groups of the post-Palaeozoic and the lamellar character of the hyaline group.

These observations led to a comprehensive reclassification by Carpenter (1861, 1862). Two suborders were recognized: Imperforata, to include membranous, 'porcellaneous' (porcelaneous) and 'arenaceous' (agglutinated) families and the Perforata, taken to include three calcareous families – one finely perforate (Lagenida), one coarsely perforate (Globigerinida) and one finely perforated with canal system and supplementary skeleton (Nummulida). With its emphasis on fine structure and composition this classification is decidedly modern in outlook and it might be thought that simple elaboration of its main ideas would have taken place through the late nineteenth century. For a number of reasons this was not to be the case. In particular, although in outline the classification ostensibly presumes a necessary connection between wall structure and perforation, detailed perusal reveals a major contradiction. The tendency of some 'rough-cast' porcelaneous miliolids to acquire an outer agglutinated coat was considered 'a trifling variation', not justifying their separate treatment. Similarly, perforate agglutinated forms with calcareous cement were

united with their calcareous homeomorphs and (1862, p. 48) separated from 'proper...purely arenaceous' forms with organic cement in which 'the absence of any pseudopodial pores...shows their affinity to be rather with the porcellaneous than with the hyaline series'. In this way, Carpenter tried to rationalize a system based on the idea of the primacy of perforation as an indication of fundamental physiological distinction, but at the cost of considerably devaluing wall composition as well as chamber arrangement. It is interesting that in claiming that the porcellaneous and hyaline series are isomorphic in chamber arrangement he overlooked the distinctive milioline coiling of a major proportion of the porcellaneous group, including the 'rough cast' forms which could have assisted his argument. Quite apart from this contradiction at the heart of the classification, the very success of the rhetoric of the founder members of the English School regarding the impossibility of recognizing species on the basis of the hard parts (if at all) helped to undermine it from the start. Thus, ironically, despite its brilliant insights, it came to be seen as over-elaborate, like the parallel scheme of Reuss (1862), also based on the discoveries of the English School, but with twenty-eight families recognized.

The triumph of the English School

These changing ideas were well shown by the new classification proposed by Brady (1884), on the basis of comprehensive collections from all the major oceans, made during the voyage of the *Challenger* (1872–74).

Although during the intervening years there had been an attempt to solve the problem of the relationships of perforation and wall composition by putting composition at the higher hierarchical level (Rupert Jones 1875), Brady considered this 'cutting rather than untying the knot', and abandoned 'minute structure' as a means of subdividing the order as 'not uniformly applicable'. Carpenter's six families were refined and increased to ten (including twenty-nine subfamilies) with much more emphasis on chamber arrangement, particularly evident at subfamily level. Also, against the spirit of Carpenter's 'Principles', the unilocular family *Astrorhizidae* was set up to cover single chambered agglutinated genera from the Abyssal Plains and the *Globigerinidae* was restricted to planktonic genera. However, the family *Textulariidae* was still considered to include both agglutinated and hyaline, biserial and triserial genera. The Lyellian steady-state, uniformitarian dogma of the English School is also apparent in the idea that *Nummulites* ('*Nummulina*') ranged back to the Carboniferous, in the inclusion of *Fusulina* in the same family, and in the failure to separate *Endothyra* from the agglutinated group.

The continuing confusion about species was also still evident. On the one hand Brady quotes Carpenter's views with approval and states 'so-called species represent no more than terms of a series', but on the other hand he recognizes (p. vi) 'modifications...whether species or not which differ not merely in details of form and structure but in habit...with characters that afford means of easy identification'. The attempt to group varieties around a few primary types was abandoned and the treatment of species and genera is nearer to that of Reuss and the Continental School. Despite the continuing disagreement about stratigraphical ranges, it is possible to see here the beginning of a rapprochement, although Brady's species limits are extremely wide and he found the 'needless multiplication' of species by European workers 'a bar to progress'. In the event, reconciliation between the two schools lay well into the next century.

Brady's simple classification, backed by the beautiful lithographed plates in the *Challenger* Report (unsurpassed until the invention of the scanning electron microscope and still superior in some respects), was widely influential and remained in use, modified by Lister (1903), almost into our own day (Jepps 1956). This reflects the long dominance of the English School and the apparent confirmation of its views: first, by the detection of pores in the proloculus of the porcellaneous genus *Peneroplis* (Rhumbler 1895); second, by the discovery of calcareous genera, in supposed Cambrian limestone from Malvern, some specimens actually being put into three extant species by Chapman (1900). The issue of the 'Cambrian' calcareous foraminifera became the 'cause célèbre' of foraminiferal studies, not solved until Wood (1947) demonstrated that the fauna was derived from an erratic of early Mesozoic age. Meanwhile workers like Galloway (1933) and Chapman and Parr

(1936) who tried to take the occurrence into account in classification, were almost bound to decide that calcareous forms sprang from tectinous ancestors and that agglutinating forms arose later and were more advanced. The germ of this idea may be found in Carpenter (1862). Those that did not, like Cushman (1927), who on the basis of his stratigraphical work had good reason to find it suspect, were forced to try and explain it away as a result of post-mortem calcification. Inevitably, wall structure was further devalued to the point that Douvillé (1906) decided it was determined entirely by habitat.

Economic imperatives and the rise of the American School

It is interesting historically, that just as the philosophy of the English School apparently reached its apotheosis, developments elsewhere in the world, in particular, the successful application of larger foraminifera in the Far East and the Caribbean, and of smaller foraminifera in the oilfields of Texas, vindicated their use as biostratigraphical index fossils.

The name chiefly associated with the taxonomic work on the great number of new genera and species that now came to light was that of Joseph Cushman, the key figure in what came to be known as the American School (Galloway 1928). He began his career working mainly on Recent Foraminifera, indeed his interest in them continued until his death (Cushman 1932, 1933, 1942) and his knowledge was as extensive in this area as that of Brady. But he also became well known as a consultant for the U.S. Geological Survey and various oil companies. This allowed him to set up his own laboratory in 1924 and to begin the serial publication of the famous *Contributions from the Cushman Laboratory for Foraminiferal research* which attest to his unrivalled knowledge of foraminifera from both the subsurface and outcrop. With this background he was well suited to syncretize the philosophies of the English and Continental Schools and to mitigate their tendency towards excessive lumping on the one hand and excessive splitting on the other. This was not achieved immediately because the sheer volume of new material necessitated the creation of many new taxa and this was fiercely criticized by members of the English School, still labouring under the misapprehension that the fauna from the Malverns was Cambrian and clinging to Carpenter's central dogma: that the Foraminifera were a simple plastic group.

The initial reaction of the English School is well shown by Heron-Allen's review (1929) of Cushman's new classification (1927, 1928) which recognized some 600 genera (compared to the 141 of Brady), 'an overwhelming avalanche' causing the 'brain of the beginner to reel'. In particular, he deplored the splitting of many genera, with the revival of many of d'Orbigny's names, as well as previously abandoned names. Although admitting that the time had come for an 'exhaustive' reclassification, he was 'assailed by doubt' in his response to the argument for splitting based on stratigraphic utility and as well as pointing out the problem of facies, suggested that unconformities and faults could 'seriously embarrass' the petroleum geologist and that it was 'self-evident that the pelagic Foraminifera must be useless as stratigraphical indications'. That the battle was now between applied and academic workers rather than schools is revealed by later correspondence in *Nature* (Heron-Allen 1935) where he quotes Hans Thalmann's description of the creation of new genera and species in 1933 and 1934 (more than 300 per annum) as '*dementia nomenclatorica americana*'. It is interesting that, despite quoting Thalmann's remarks with apparent approval, he admits the responsibility of Earland (his co-worker on the *Discovery* material) for seventy-three of the new species for 1934. This contradiction is reminiscent of Brady who similarly found it necessary to legitimize his own taxonomic offspring by appealing for general adherence to the standards of rectitude set by the early Fathers of the English School.

Cushman not only increased the number of genera to some 600 but replaced earlier groupings by forty-five families (many based on the subfamilies of Brady) which were increased to fifty in the last edition of his book, *Foraminifera* (1948). These families were clearly distinguished on grounds of wall structure as far as it was then known, chamber arrangement and aperture form, with coiled genera regarded as leading to uncoiled genera. Unilocular agglutinating forms were considered the most primitive group and ancestral to most other families via coiled, unilocular genera already present in the Lower Palaeozoic. In his general acceptance of ontogeny and recapitulation as a key

to unlock the phylogeny of multiform species, and of uncoiling as a dominant trend, he followed Lister (1903) and Schubert (1908, 1921) rather than Rhumbler (1895, 1911, 1923) and Douvillé (1906) who believed in proterogenesis and general coiling-up. There is an interesting correspondence here with the rejection by Spath (1933) of the idea of a general, coiling-up trend in the cephalopods as postulated by Hyatt (1900).

Like Brady, Cushman did not group his families in phylogenetic lines (probably because of the difficulties caused by the confused stratigraphical evidence) but fifteen of the calcareous perforate families were regarded as having common descent from a roataliid ancestor. As was shown by Wood (1949), apart from *Peneroplis* and its allies which Cushman separates from other porcelaneous forms on the groups of their postulated perforate ancestry, his families can be grouped into distinct higher categories based on wall structure. That this was not done reflects the continuing doubts about the importance of wall structure and the persistence of the idea of the primary importance of perforation. Cushman also followed Brady in including the Palaeozoic endothyrids with the agglutinating litiolids.

The families were grouped into higher categories by Glaessner (1945) who recognized seven superfamilies based on wall structure, chamber arrangement and apertural form. The endothyrids were placed in a separate superfamily with the fusulines on the grounds of their microgranular wall structure (Henbest 1937) and the porcelaneous families were also regarded as a natural group originating from a coiled unilocular ancestor. Glaessner laid particular stress upon the value of biological studies in interpreting the fossil record and pointed out how the work of Myers (1935, 1936), Le Calvez (1938) and Jepps (1942) not only clarified problems of dimorphism and reproduction, but proved the stability of species and of wall structure, perforation and chamber form under different ecological conditions. However, although the superfamilies were considered to have a common origin in coiled, unilocular, agglutinated ancestors, the continuing existence of the 'stumbling block' to confident phylogenetic work, created by the supposed Cambrian fauna of the Malverns, meant that no attempt was made to recognize suborders on the basis of wall structure.

The return to wall structure as the primary basis of subdivision

Wood (1947, 1949) not only removed the 'stumbling block' in the way of recognition of the stratigraphical succession of the major groups of Foraminifera but greatly clarified knowledge of wall structure. The optical characteristics of the main types were clearly defined and the hyaline group was shown to include both radial and oblique ('optically granular') genera. It also encouraged other work on fine structure which with the help of TEM now proceeded apace, leading to the suggestion there were three types of lamellar wall, monolamellar, monolamellar with septal flap and bilamellar (Smout 1954; Reiss 1958, 1965). This microscopical work on fine structure is reminiscent of that of the early English School and in the same way came to underpin a new classification, that of Loeblich and Tappan (1964), the most important and widely followed of those proposed in the wake of the great expansion of foraminiferal studies during and immediately after the Second World War. Compared with Cushman's scheme the number of genera and families was practically doubled, to 1194 and 95, grouped in seventeen superfamilies and five suborders. The outcry that greeted the appearance of Cushman's classification was not repeated in the case of that of Loeblich and Tappan. Although Berggren in his review (1965), remarked that few could have been prepared for the appearance of such a 'two volume tome' he went on to say that comparison of the numbers of taxa recognized with those in other invertebrate groups, revealed it was actually conservative. It is also significant that the main criticism made by Lee (1966) in his review of the biological section, is of the assertion that 'the simpler genera' with a single-chambered test of pseudochitin or pseudochitin combined with agglutinated particles also have simpler histories, remarking that the life cycle in *Allogromia* is complicated and indicates the opposite. This general change in attitudes was largely due to the influence of Cushman's book, which went through four editions, to the impact of biological work, and to the successful stratigraphical application of larger, smaller and planktonic foraminifera in the subsurface (in which British micropalaeontologists fully participated, particularly in the Middle East and Caribbean). Although problems of definition

remained, the 'new synthesis' between population genetics and Darwinism in the 1930s and 1940s established the modern species concept and thereafter the debate was between individuals rather than schools. The idea that foraminifera were a simple, plastic group in which true species did not exist largely disappeared.

Wall composition and fine structure were now regarded as most important and the basis for recognition of the suborders and superfamilies, with apertural characters and chamber arrangement second and third. Thus we find that, after just over a hundred years, wall composition and fine structure have returned to favour, on the lines of Rupert Jones's attempted revision of Carpenter's scheme with perforation made subordinate:

- Allogromiina – membranous
- Textulariina – agglutinated
- Fusulinina – microgranular
- Miliolina – porcelainous (imperforate in post-embryonic stage)
- Rotaliina – calcareous perforate

Apart from the microgranular group, the major subdivisions are based on the wall structure categories of Williamson, and reliance on wall composition and layering is carried to great lengths in the recognition of the superfamilies. In particular, aragonitic, calcitic spicular, calcitic single crystal and hyaline-oblique ('optically granular') structures were given superfamily status. However, the attempt to use wall structure as a key led to inherent difficulties like those in Carpenter's scheme. Although the Rotaliina were defined as calcareous perforate and the Miliolina as imperforate in the post-embryonic stage, separate status was not given to the perforate families in the calcareous microgranular group or to those in the agglutinated group (also discounted by Carpenter). Again, although aperture form is stated to be more important than chamber arrangement, in practice, the lower divisions were recognized on a combination of characters, and where wall structure and apertural changes with ontogeny were ill-understood, chamber arrangement inevitably took precedence.

History also repeated itself in that opinion swiftly swung away from the extremes of this mid-twentieth century cutting of the Gordian Knot. Towe and Cifelli (1967) showed that although radial and hyaline-oblique structure are distinct optically they are close crystallographically, and one may easily give rise to the other. Indeed, intermediate forms have been shown to exist (Bellemo 1974). This confirmed the variation noted at the specific and generic level in many families by Haynes (1956) and Wood and Haynes (1957). It thus became clear that the Cassidulinacea was an artificial grouping and that wall structure shows progressive changes in many groups, e.g. in the Elphidiidae and Cibicididae (Anomalinidae) where chamber arrangement remains stable, in contrast to the Nodosariidae in which wall structure is stable while chamber arrangement shows rapid progressive change along many lines. Similarly, the attempt to subdivide the hyaline group on the basis of layering ran into problems of conflicting observations until it was decided that all the Rotaliina, apart from the monolamellar Nodosariacea were bilamellar (Hansen and Reiss 1972; Grönlund and Hansen 1976). Some of these problems were taken into account by Loeblich and Tappan in various modifications of their scheme (1974, 1984). In particular, in 1974, they abandoned the attempt to make hyaline-oblique and bilamellar structure the basis of separate superfamilies, although wall composition was retained as the basis of the overall grouping.

The *Treatise* classification became the dominant influence on foraminiferal studies for more than two decades. Of other classifications proposed, the most interesting was that of Hofker (1951) in which the hyaline foraminifera, considered to be derived from agglutinated forms with a toothplate, are divided into three suborders:

- Protoforaminata – single aperture, finely perforate (protopores)
- Biforaminata – two apertures, finely perforate
- Deuteroforaminata – secondary aperture dominant, coarsely perforate (deuteropores)

Unfortunately, although this arrangement emphasizes the aperture and internal characters and

brings perforation back into consideration as a major factor, it largely ignores wall structure and stratigraphical relationships and although modified by Reiss (1958) has not been followed.

The classification of Haynes (1981) retained wall structure as the major consideration at the higher level but with recognition of nine orders and a return to class distinction. The hyaline group was considered polyphyletic and broken into five orders, e.g. the Buliminida were considered to have been derived from high trochospiral agglutinated forms (following Hofker in echoing Carpenter) and the 'vitreous' Palaeozoic genera were separated as a suborder within the microgranular group. The superfamilies were recognized on a combination of coiling mode and apertural form and emphasis was placed on umbilical characters. A major weakness is that perforation is ignored and the presence of pores in the megalosphere of *Peneroplis* is dismissed (along with the much more doubtful 'pores' in the walls of adult peneroplids and miliolids). This leads to the contradiction that although the hyaline group is regarded as polyphyletic, porcelaneous genera are considered to constitute a natural group. Further contradictions are that milioline agglutinating genera are left within the Miliolida (as by Brady) and that the single crystal Spirillinacea are considered the possible rootstock for the microcrystalline Rotaliida, although the genome is apparently more complex in genera such as *Patellina* than in simple discorbaceans.

Summary

This review of the most influential of past classifications reveals: the baneful influence of the idea that the Foraminifera are a very simple, plastic group; the strong influence of ideas about species on classification and biostratigraphical use; the uncertainty about the value of wall composition and fine structure until biological studies showed modern species to be stable and the stratigraphical relationships of the major groups were clarified. It is also clear that use of a single factor at the higher hierarchical levels, cuts rather than unties the Gordian Knot, as Brady remarked, i.e. a solution likely to be as short-lived as Alexander's empire. In this respect, it is interesting to see how well the new classification of Loeblich and Tappan avoids the pitfalls of the past.

THE NEW CLASSIFICATION OF LOEBLICH AND TAPPAN (1988)

The period since the publication of the classification in the *Treatise* of 1964 has been a time of unprecedented growth in foraminiferal studies, especially as applied to subsurface stratigraphy by the oil companies and to the core material made available since the initiation, in 1968, of the Deep Sea Drilling Project which has triggered an explosive outburst of activity on planktonic groups. The providential, commercial appearance of the Scanning Electron Microscope, at almost the same time, has also allowed more accurate discrimination of taxa on the basis of internal, apertural and external features, leading to the recognition of large numbers of new genera. In addition, many of those synonymized in 1964 are now regarded as distinct. This has brought the total number of genera considered acceptable by Loeblich and Tappan in 1964 (1,192) to more than double that figure in 1988 (2,446). These have not just been added to existing suprageneric taxa, as might be expected in a 'relatively stable' classification, because these categories have also more than doubled: suborders (5 to 12); superfamilies (17 to 65); families (95 to 296); subfamilies (129 to 300). This is not only because of the discovery of new supra-generic taxa but also because of the higher weighting now given to certain criteria as compared to their approach in 1964. This explains why the number of families has trebled and the number of superfamilies almost quadrupled, although the number of genera has little more than doubled. A possible cause for concern is that fifty-six of the subfamilies, forty-four of the families, three of the superfamilies (two in open nomenclature) and two of the suborders are represented by one genus only (105 taxa in all). A simple explanation is that many genera cannot be placed close to existing taxa because of the incomplete (as well as incompletely known) stratigraphic record. Alternatively, it may be argued that the group is being oversplit. Probably both tendencies are at work. The large number of families recognized is clearly important for macro-evolution, presuming that 'the taxonomic family is the conventional unit for studies of large scale extinction and rates of change of diversity' (Newell 1982, p. 260). It may also

be considered encouraging that the average number of genera per family is 8.26 which falls between the 5 to 10 considered the general average by Van Valen (1973) presuming these numbers are not artifacts and are telling us something about niche partitioning. This may also suggest that the families and subfamilies with very high numbers are probable candidates for further splitting, if we consider that ideally a subfamily should represent a single evolutionary lineage, e.g. thirty-seven genera are included in the subfamily Miliolinellinae. However, there will clearly be differences according to whether evolution in the family is dominantly allopatric and branching, or sympatric and phyletic.

Criteria employed at generic level

As the title suggests, the work was conceived as a handbook of genera. There is a prodigious number of excellent plates and most genera considered synonymous are also illustrated. The success of the authors in carrying out this massively daunting task, is attested by the comments of reviewers: thus Banner (1988) considered it 'virtually miraculous' that not only had they managed to complete the task but had 'done it very well'; and Haman (1988), although he regretted that 'rigorous criteria were not used', considered the work a 'scholarly endeavour', and a 'useful, well-illustrated catalogue'. The reaction to the decision not to recognize subgenera was more mixed. Although approved by Haman, Banner considered recognition would have helped to diminish the rigidity of the generic diagnoses and Jenkins (1989) that they are essential to show iterative, evolutionary lines. Adams (pers. comm.) has also pointed out that subgenera have been raised to full genera without discussion, as in the case of the Lepidocyclinidae (see Adams 1987a).

Although it is not made explicit, the genera are recognized on the basis of test architecture and coiling mode, aperture form and accessory structures and internal structures. The authors also carry through the presence/absence of keels, umbilical bosses and supplementary apertures as generic criteria much more consistently than in the *Treatise*. An important innovation is the use of ornament at generic level, following its successful use recently in the planktonic forms. The well known *Lingulina tenera* plexus of the Lias is thus transferred to *Paralingulina*. Although this may cause raised eyebrows, the re-instatement of many genera previously put in synonymy is to be generally welcomed. A good example is that of *Ornatanomalina* from the Palaeocene of Pakistan, formerly put in synonymy with *Thalmannita*, described from the Palaeocene of Cuba. This led to widespread records of *Thalmannita madrugensis* in Africa and Europe which on inspection are found to refer to species of *Ornatanomalina* (Haynes and Nwabufo-Ene 1988). This perfectly illustrates the palaeogeographical importance of refinements in taxonomy. A common fault in palaeontology (which also tends to bring taxonomy into disrepute) is the confusion of a diagnosis with a full palaeontological description. As pointed out by Banner (1988), this is not avoided here. In fairness to the authors, they have obviously tried to include all the features that may be relevant, including in some cases long accounts of reproduction. But this means that the reader has to search, often vainly, for the distinguishing features of the genus amongst specific details and repeated suprageneric characters sometimes, but all too rarely, finding what is required only under the Remarks. A minor point, but a possible source of confusion, is the continued use of spiral and umbilical as descriptive terms for the dorsal and ventral sides of the test. As both sides in a trochoid test are spiral (and may be umbilicate) the older terms are much to be preferred.

Criteria employed at the suprageneric level

Predictably, the reaction to the changes at suprageneric level have been more adverse. Thus Haman (1988) who provides a synopsis of the main taxonomic changes, considered the 'rationale not easily determined', and some of the family distinctions only generic. He clearly felt the new scheme inferior to the 'incisive and decisive' classification of the *Treatise* and that 'desired stability had not been achieved'. Banner (1988) was also 'unhappy about some of the concepts... and the suprageneric importance... given to some morphocharacters'. How far can these criticisms be sustained?

Loeblich and Tappan have had the problem of revising their suprageneric arrangement at the same time as incorporating a large number of new genera. They have made their task somewhat harder by continuing to cramp the Foraminifera within one Order, following Levine *et al.* (1980), a procedure that looks increasingly outdated in the light of the statement by Sleight (1989) that the amoeboid protists comprise a number of evolutionary lines and are 'almost certainly polyphyletic'. Margulis (1974) has even suggested the Foraminifera should be considered a phylum. Upgrading them at least to class or subclass status would seem to be warranted by their position as the largest and most varied group of invertebrates and unique style of reproduction, with, like plants, a diploid asexual generation.

The five suborders of the *Treatise* are now increased to twelve:

Allogromiina	organic wall, unilocular (may tend to multilocular)
Textulariina	agglutinated
Fusulinina	homogeneously microgranular
Involutinina	aragonitic, non-septate
Spirillinina	calcitic, single crystal, non-septate (may have few chambers)
Carterinina	spicular, secreted calcite crystals
Miliolina	porcelaneous imperforate, true pores in protoconch of some
Silicoloculinina	opaline silica, imperforate
Lagenina	calcitic, hyaline-radial, monolamellar
Robertinina	aragonitic, hyaline-radial, septate, internal partitions, finely perforate
Globigerinina	calcitic, hyaline-radial, perforate, bilamellar, planktonic.
Rotaliina	calcitic, hyaline-radial or oblique, perforate, bilamellar, benthonic.

This breakdown reveals the authors continued reliance on wall structure at this level, though there are inconsistencies. Two, the Globigerinina (planktonic habit) and the Lagenina (fine structure of lamellae), are recognized on other criteria which leaves the Rotaliina inadequately diagnosed. On this basis the buliminids also merit equal recognition and separation from the rotaliids. The Fusulinina are defined as microgranular but include the Archaeodiscacea and Colaniellacea, described as having radial layers, and included in the Archaeodiscina by Haynes (1981). Other difficulties include separation of the non-septate, aragonitic group, as the Involutinina, from the septate Robertinina, whereas in the Allogromiina, Spirillinina and the Textulariina, non-septate and septate forms are included together. Agglutinated genera with milioline coiling (Rzehakinacea) are included in the Textulariina but their relationships with miliolids in the Recent (Haynes 1973) and first appearance in the Lower Cretaceous associated with acidic and low oxygen environments suggests a separate origin from within the Miliolida, dentate forms via the Miliolacea, edentate forms via the Ophthalmodiacea. The single species, *Miliammina legis*, included in the supposedly siliceous Silicoloculinina may represent a similar response, in this case to life below the Calcite Compensation Depth (CCD) by agglutination of siliceous rods. The Carterinina is also based on a single genus in which the test is composed of calcareous spicules. However, these were regarded as agglutinated by Brönniman and Whittaker (1983). Perhaps *Carterina* should have been placed under 'Genera of Uncertain Status' pending the necessary tank studies.

The features now considered important at superfamily level are the unilocular, bilocular or multilocular character of the test, presence or absence of perforation, canals and major apertural features. Bilocular is not defined in the glossary and generally includes non-septate forms in which the initial end is expanded to form a cavity, considered homologous with a proloculus in septate forms. Non-septate multilocular forms, where the chambers are connected by stolons, are not separately considered. Family features now include free or attached habit, presence of internal subdivisions and surface texture as well as coiling mode. Because they regard wall structure as more fundamental than number and arrangement of chambers, both of which may change during ontogeny and therefore being more indicative of evolutionary relationships, they (paradoxically) tend to discount ontogeny as a key to phylogeny at the highest levels so that coiled, uncoiled, uniserial and unilocular genera tend to be put in separate groups. For instance, fully uniserial agglutinating genera are separated from those which become uniserial in the adult and regardless of apertural style are included in a single superfamily, the Hormosinacea.

They may have been unduly influenced here by the current, fashionable revival of the idea of a general coiling up trend involving proterogenesis, as against uncoiling involving recapitulation; exemplified by Brasier's attempt (1982) to show that the overriding imperative in the evolution of test architecture is towards minimum lines of communication between proloculus and aperture ('MINLOC'). This idea is somewhat weakened by the observation that the soft parts are generally confined, or retract into, the penultimate chamber. Their approach makes particular coiling modes 'stable' by default and produces a horizontal arrangement. On the whole, forams show new features in the adult and the stratigraphic record provides evidence of repeated uncoiling trends with connected serial changes in aperture form and position. The ideal shape for rapid movement through sediment by retraction of the podostyle directed forwards from a terminal aperture is apparently reached in many unrelated lines of smaller deep-sea forams. Recognition of these lines would have simplified the classification at family and superfamily level, especially if the difficulties encountered by the authors at the subordinal level were eased by the recognition of orders (as by Haynes 1981). It would also have helped to remove some of the inconsistency inevitable in horizontal groupings of a class that exhibits rapid evolution with serial development of all features of the test at some time, usually in combination. The only

'key' to these developments is the stratigraphic and evolutionary record and it cannot be predetermined. To be fair to the authors much of the inconsistency arises because of the different levels reached by research into different families. The Nummulitidae, probably the most famous fossil forams, are a good case. In the *Treatise* (1964), Cole lumped most of the genera previously recognized under *Nummulites* because they grade into each other. This extreme lumping, neo-linnaean in its search for morphological gaps, pleased no-one, except perhaps, punctuationists convinced that evolution proceeds by genuine saltations ('hopeful monsters'). Most of the genera remained in use and are reinstated in the present work. However, genera with subdivided chambers, even the sub-annular complex form *Spirochypus*, are included in the same family, rather than being separated as Cycloclypeidae (Haynes 1981) though this would be consistent with their own criteria. Already since publication, the wave of research has undermined this systematic sand castle. Adams (1988) has shown that the type species of *Nummulites* has secondary chamberlets and Haynes (1988) has redefined *Ranikothalia* with revival of *Nummulitoides*. This illustrates how the numbers of taxa recognized (diversity) varies not only with the data available but also according to the current philosophical paradigm and underlines the futility of pious prayers for 'stability'. As Knoll and Butterfield (1989, p. 602) wrote recently, 'Taxonomic changes both reflect and influence the way we think about evolutionary pattern and process'.

A review of the treatment of major suborders will indicate some of the difficulties to be overcome, especially necessary considering the use already made of the taxa recognized (in the evolutionary and diversity study published by Loeblich and Tappan 1988b).

Problems in the treatment of the suborders by Loeblich and Tappan (1988a)

Allogromiina. Although the naked Allogromiina are defined as membranous or proteinaceous, the included families Lagynidae and Allogromiidae are defined as being both, the Allogromiidae as proteinaceous on a plasma membrane. Within the Allogromiidae the only difference between the subfamilies Sheppardellinae and Argillotubinae appears to be that the Argillotubinae are wrinkled and may be fixed.

Textulariina. Within the non-septate, agglutinating superfamily Astrorhizacea the only difference between the family Astrorhizidae and the Rhabdamminidae, as defined, appears to be the greater selectivity shown by the latter, because *Rhabdammina* also has branches leading off a 'globular central area'. The Rhabdamminidae also includes both free and fixed forms, in contradiction to the stated criteria. In the remarks on the sub-family Halyphyseminae the comparison is presumably being made with the Dendrophyrinae, not Rhabdammininae. The family Psammosphaeridae is defined as coarsely agglutinated but the subfamily Psammosphaerinae as finely to coarsely agglutinated. *Technitella* is figured upside down and on the basis of the spicular wall and the broken attachment end (Haman 1967) mistaken formerly as the aperture, should be transferred from the family Saccaminidae to the Rhabdamminidae, subfamily Halyphyseminae. No clear distinction is made between the family Hemisphaeramminidae and the Saccaminidae and Psammosphaeridae. The Diffusilinae is defined as being distinguished by an irregular mass of branching tubes but this does not agree with the diagnosis of the two genera included. There is no mention of tubes in *Diffusilina*.

The superfamily Hippocrepinacea is defined as possessing a proloculus and tubular or flaring second chamber. However, the subfamily Hippocrepininae does not show a proloculus initial end and the Notodendrodidae (one genus) actually has a bulbous central region leading to tubular arms. Within the planispiral to uncoiled superfamily Lituolacea, the family Lituolidae is defined by possession of simple interiors and terminal apertures which is taken to differentiate them from the Discaminidae which is diagnosed as having internal partitions, i.e. secondary septa. However, the figures given of *Discamina* and *Ammoscalaria* seem to show primary septa (organic without agglutination) only, with no subdivision of the chambers. There seems little reason to separate them from *Eratidus* and other genera included in the Lituolidae, subfamily Ammomarginulininae. Also, it is not clear why a simple wall is considered important in the definition of most of the families and subfamilies when it is not mentioned in the superfamily definition and no cases of complicated walls are included. No reason is given for including the Adhaerentiinae which lack an initial coil and are biserial, in the superfamily.

Although the superfamily Haplophragmiacea is defined as streptospiral to uncoiled, it includes the streptospiral to planispiral Recurvolidinae (as a subfamily of the streptospiral Ammosphaeroidinidae). It also includes the calcareous trochospiral and planispiral families Nezzazatidae and Barkerinidae. (Note that although the Nezzazatidae are defined as trochospiral to planispiral, the subfamily Nezzazatinae is defined as trochospiral or planispiral.) These families, with their digitate internal partitions and areal apertures, may represent diagenetically altered robertinids. They are certainly not close to *Ammosphaeroidina*.

The family relationships within the superfamily Cyclolinacea are not made clear and the diagnosis given for

the family Orbitopsellidae does not adequately distinguish it from the Cyclolinidae. The terminology used here, as in the case of the Loftusiacea (inherited from previous workers it must be said) is not helpful and the fog-index is high. The family Cyclamminidae is defined as involute and rarely uncoiling, yet it includes the subfamilies Pseudochoffatellinae (evolute) and the Choffatellinae (only one out of eight genera with no tendency to uncoil). Neither the subfamilies Alveophragmiinae nor the Hemicyclamminae seem to be adequately diagnosed on the criteria given.

The superfamily Spiroplectamminacea is defined as planispiral to biserial and uniserial development is not mentioned (nor is streptospiral coiling) although the family Spiroplectamminidae is defined as planispiral or streptospiral to biserial, rarely becoming uniserial. In fact, two of the eight members of the Spiroplectamminae become uniserial and both the genera placed in the Vulvulininae. Three of the seven genera placed in the family Textulariopsidae become uniserial and one of the three placed in the Pseudobolivinae. It is not possible to distinguish between these two families on the criteria given.

The subfamily and family distinctions are not clear in the diagnoses given for the superfamily Pavonitinae. This group may be of polyphyletic origin.

Within the superfamily Trochamminacea the sub-family Trochammininae are diagnosed as 'trochospiral or may tend to uncoil'. None of the ten genera included and illustrated shows uncoiling.

All the canaliculate, high trochospiral agglutinating genera are included, with the biserial Textulariidae, in the superfamily Textulariacea and the non-caliculate genera are accommodated in three other superfamilies. Because this emphasis on perforation tends to cut across groupings made on other features the superfamilies show a mixture of coiling modes and apertural styles. The Verneuilinae and Ataxophragmiacea are not actually distinguishable as defined and it must be pointed out that the family Prolixoplectidae are included in the Verneuilinae on the assumption they are non-caliculate but the fine structure is only known in three of the nine genera. A number of families in the Ataxophragmiacea are defined as possessing a two-layered wall but the terminology is confusing. In the family Textulariellidae 'beams and rafters' are said to produce an 'alveolar wall'. In the Dicyclinidae there are 'transverse or radial partitions'. The Dictyopsellidae have a 'sub-epidermal network', and partitions are not mentioned, but in the Pfenderinidae, 'vertical or horizontal partitions' result in a 'reticulate subepidermal layer'. However the wall structure is defined, these families do not appear to be close to the Ataxophragmiidae and the family Cuneolinidae (which includes *Sabaudia*, characterized by a double-walled embryo with microgranular inner and radial outer layer) probably does not belong here either. The Coskinolinidae appear more closely related to the superfamily Orbitolinacea. They have been excluded because they lack marginal exoskeleton (marginal subepidermal partitions). They are also stated to lack the embryo of protoconch and deutoconch diagnostic for the subfamily Dictyoconinae but that feature has only been found in eight of the twenty six genera included.

Within the superfamily Textulariacea the subfamily Minouxiinae in the family Eggerellidae is defined as cribrate which conflicts with the definition of the Dorothisinae as also developing multiple apertures and which includes *Arenodosaria* in which the aperture is described as sometimes becoming cribrate. The definition of the family Pseudogaudryinidae is incomplete, the aperture being described as an interiomarginal arch with the trend to multiple apertures not included.

Fusulinina. Within the Fusulinina, defined as 'homogeneously microgranular', the unilocular Parathuramminacea is divided into families mainly on the number of layers and character of the wall. However, the Parathuramminidae appears to be distinguished from the Chrysothuramminidae by wall thickness alone.

The superfamily Moravamminacea which includes genera with proloculus and tubular second chamber is distinguished from the Earlandiacea simply on the basis of the appearance of incipient septa and otherwise shows a very similar range of morphology. The distinctions as defined between the families in the two groups are not clear. The Earlandiidae are not distinguished as straight but defined as free, although *Warnantella*, put in the Pseudoammodiscidae, may be free. Both the Pseudoammodiscidae and Pseudolituotubidae include streptospiral forms. The Caligellidae, defined as curved to straight, includes genera showing initial coiling and therefore cannot be distinguished from the Moravamminidae.

As defined, the Tourneyellacea cannot be distinguished from the Moravamminacea and the definition actually should exclude the subfamily Palaeospiroplectamminae which would be better placed within the family Palaeotextulariidae.

The definition of the superfamily Archaediscacea does not make a clear distinction from these two superfamilies either, because the appearance of a 'radially built' outer wall layer in this group is only introduced in the family diagnoses. Inclusion of this superfamily in the Fusulinina clearly offends the stated criteria as does the inclusion of the Nodosinellacea 'fibrous inner layer', the Geinitzinacea 'radially fibrous' outer layer and the Colaniellacea outer 'vitreous' layer. The imprecision of this terminology and the

description of the Nodosinellidae as 'fibrous or perforate', suggests that more detailed research is required into this whole group and that perpendicularly arranged granules without optical alignment (fibrous structure as in *Palaeotextularia*) is being confused with radial hyaline structure.

The superfamily Endothyrea is not defined as multilocular or septate, although they follow the Tourneyellacea, and although most of the genera show streptospiral to planispiral coiling with growth the superfamily and the family Endothyridae and the subfamily Endothyrinae are defined as 'planispiral to streptospiral'.

The coiling mode in the superfamily Fusulinacea is not given in the superfamily definition. In the definition given for the family Ozawainellidae it is stated that geological early taxa are planispiral and evolute but three of the four Carboniferous genera are involute and only *Pseudonovella* is evolute with the final whorl enveloping. This genus should probably be removed to the Loeblichidae. This weakens the supposed distinction between the Ozawainellinae and the Pseudostaffellinae and between the Ozawainellidae and Staffellidae. The presence of early streptospiral coiling is inadvertently left out of the definition of *Pseudostaffella*. Within the Fusulinidae the distinction between the subfamilies Fusulinellinae and Wedekindellinae is not clear. Within the Schwagerinidae the subfamily Chusenellinae is defined as possessing plane or weakly folded septa in the early stage but both the genera described have plane septa initially. The definition of the Verbeekinae does not include the vital information that the septa are plane (only given in the case of the subfamily Pseudodoliolinae). The subfamily Kahlerinae, defined as small with single tunnel, does not fit the family definition.

Miliolina. Within the superfamily Cornuspiracea the distinction between the family Cornuspiridae (planispiral to streptospiral) and the Hemigordiopsidae (streptospiral to planispiral) is not clear. This is because the subfamily Meandrospirinae (planispiral or streptospiral) is included in the Cornuspiridae. Also, as defined, the Meandrospirinae do not appear to be separable from the Calcivertellinae. Genera in which incipient chambers and definite septation appear in the adult whorls are included in the Baisalinidae and those with a few chambers throughout, and definite flexostyle, in the Fischerinidae. However, *Dolosella* in which the holotype has several undivided whorls, is included in the Fischerinidae. The subfamily Spiriamphorellinae is defined as like *Ophthalmidium* in the early stage. If so (the type figures are obscure) it cannot be included in the Nubeculariidae, as defined.

The definition of the superfamily Miliolacea which rests entirely on coiling mode does not exclude the Ophthalmidiidae and other forms with chambers of half-coil length included in the Cornuspiracea. This also applies to that given for the family Hauerinidae because genera with simple apertures without teeth are not excluded. Because the authors have now defined the family Miliolidae on the basis of its pseudoporous wall, simple wall structure should have been included in the diagnosis of the Hauerinidae. Quinqueloculine genera are included in the Miliolinellinae, so the distinction with the Hauerininae is not clear. The Riveroinidae are defined as planispiral but only *Riveroina* is planispiral throughout. *Pseudohauerinella* is quinqueloculine and may become planispiral in the final whorl.

The definition given for the superfamily Alveolinacea does not make a clear distinction with the Miliolacea. This is largely because of the inclusion of the Fabulariidae which are milioline. They are defined as, 'with milioline early stage' but the coiling mode in *Fabularia* and its allies is milioline throughout, the biloculine adult chambers still being added end to end. *Pseudofabularia* and *Pseudolacazina* show a fundamentally different coiling mode. The Mesozoic and Tertiary alveolines form two stratigraphically distinct groups. This is not recognized at subfamily level.

The inclusion of the family Milioporidae within the Soritacea distorts the definition of that superfamily so that it is described as 'early stage pitted or perforate and less commonly may be perforate throughout growth' which disagrees with the suborder diagnosis. However, although the Milioporidae are defined as perforate throughout ontogeny, in three of the six subfamilies it is said to occur in the outer chambers or adult and in *Kamurana*, the single genus in the Kamuraninae, it is also described as an adult character. In the other two superfamily diagnoses it is not mentioned. Although the Milioporidae are defined as being coiled in various planes (not in the superfamily diagnosis) the subfamilies show a variety of styles, even uncoiled rectilinear. *Kamurana* is described as consisting of a globular proloculus followed by an individual tube, so may have strayed in from the Cornuspiracea. The best place for this 'family' would seem to be amongst the genera of uncertain status.

Lagenina. The Lagenina are defined as radiate (as is the genus *Cryptoseptida*) rather than radial, and genera within the family Syzranidae are confusingly described as 'radial fibrous' and 'hyaline pseudofibrous' without explanation. The family Robuloididae is inadvertently described as uniserial instead of planispiral. The

diagnoses given do not make a clear distinction between the Nodosariidae and Vaginulinidae because both can include arcuate to uncoiled genera. The subfamily Marginulininae cannot be distinguished from the Vaginulininae on the diagnoses given. The inclusion of *Rimalina* with apertural slit in the Glandulininae means that this subfamily cannot be distinguished from the Entolingulininae on the criteria given.

Robertinina. The Robertinina are defined as planispiral to trochospiral and with internal partitions. However, genera which become uniserial or uncoiled biserial are included in three of the four superfamilies recognized. Only one of the three families within the Duostominacea is known to have partitions. The family Epistominidae within the Ceratobuliminacea is defined as having peripheral apertural slits but the subfamily Garantellinae is defined on the basis of its umbilical, ovate and areal apertures.

Globigerinina. The Globigerinina are defined as 'radiate' rather than radial hyaline and within the superfamily Heterohelicea, the family Guembelitridae is defined as having trochospiral, triserial or biserial early stage although the superfamily is defined as biserial or triserial which would appear to rule this family out. The family Heteroheliceidae is defined entirely on aperture form and the distinction with the Guembelitridae is therefore not clear.

The superfamily Rotaliporacea is defined as having extra-umbilical-umbilical aperture but the family Globuligerinidae have umbilical apertures as well as imperforate pustules and should probably be transferred to the Guembelitridae. Within the family Hedbergellidae the subfamily Helvetoglobotruncaninae is defined as possessing portici extending to the umbilicus. *Whiteinella*, included in the Hedbergellinae is also described as having this feature so that distinction between the subfamilies breaks down.

The superfamily Globotruncanacea is defined as having umbilical aperture and tegilla covering the umbilical area. However, in many genera the aperture is described as extra-umbilical-umbilical, e.g. *Marginotruncana*, and many are described as possessing portici rather than tegilla. The subfamily Abathomphalinae is defined as having narrow umbilicus with 'tegilla, that of final chamber covering the umbilical area'. This is inadequate considering the superfamily definition. What is presumably meant is that the tegillum of the final chamber becomes a single umbilical cover or 'techo'. Within the family Globotruncanidae, the subfamily Globotruncanellinae is defined as single keeled but genera with single keel are included in the Globotruncaninae, e.g. *Globotruncanita*, and a number become single keeled with growth.

The superfamily Globorotaliacea cannot be distinguished from the Globigerinacea as defined. The Globorotaliacea are defined as 'non-spinose, but may be pustulose or pitted', whereas the Globigerinacea 'May be covered with narrow spines'. The additional character of 'numerous small pores or fewer large ones' given for the Globigerinacea does not overcome the lack of a clear distinction. Within the Globorotaliacea smooth genera are included within the family Eoglobigerinidae, also defined as having extra-umbilical aperture without lip. However, of the four genera included only *Parvularugoglobigerina* fits this diagnosis. I agree with Brinkhuis and Zachariasse (1988) that names of this length should be excluded under the rules of the ICZN, and in this case, *Plancomusa* be substituted. The other three genera including *Eoglobigerina*, should be transferred to the Guembelitridae. As both the Globorotaliidae and Truncorotaliidae can be pustulose the distinction between these family groups is not clear. The family Pulleniatinidae is described as streptospiral. This character is not included in the superfamily diagnosis.

Within the Hantkeninacea the family Globanomalinidae includes *Globanomalina* which is low trochospiral to planispiral. This is not included in the family or superfamily definitions.

The diagnosis of the superfamily Globigerinacea does not include the trochospiral to streptospiral coiling of the included family Hastigerinidae or the areal apertures of the subfamily Orbulininae. The distinction between the Porticulasphaerinae and the Orbulininae is not clear because both can have a later enveloping or enclosing chamber.

Rotaliina. The authors subsume the Buliminida *sensu* Haynes (1981) within their Rotaliina. This leads to a very unwieldy subordinal diagnosis and attempted recognition of twenty-four superfamilies but the criteria used are inconsistent. The Bolivinitacea is reduced to two genera only. These can be distinguished from the others, removed to the new superfamily Bolivinaea only by possession of truncate and carinate periphery. Genera without toothplate are removed to the Loxostomatacea. Neither of these superfamilies would appear to warrant recognition on the authors' own stated criteria. Within the Bolivinitacea, the family Bolivinoidea is set up to accommodate one genus, *Bolivinoidea*, characterized by heavy costae, and a well known lineage in the Upper Cretaceous. However, a number of Tertiary species within the Bolivinidae show a similar type of ornament. Unless they are all to be given separate names, family distinction is hardly warranted.

The superfamily Cassidulinacea is much reduced, compared with the 1964 *Treatise*, when it accommodated

all hyaline-oblique rotraliids. Indeed, both radial and hyaline forms are now included in the family Cassidulinidae, as are genera with and without toothplates. But although *Orthoplecta* is given separate subfamily status because of possession of toothplates which make a 'spiral column', *Islandiella*, with its cornet shaped toothplate is included with *Cassidulina* in the Cassidulininae. I consider these genera, both, incidentally, radial, should be removed to the Bolivinitacea (*Islandiellidae*). The one trochoid, enrolled biserial genus known is placed in a family of its own, Cassidulinitidae but the superfamily definition does not accommodate it.

As defined, the Eouvigerinacea cannot be satisfactorily separated from the Bolivinitacea. The Lacosteinidae includes some disparate forms probably of separate origin although initially planispiral. *Lacosteina* has a drawn out 'buliminelline' adult spiral with loop-shaped aperture, while *Elhasaella* is twisted biserial with terminal aperture. Interestingly, the surface textures are quite different.

The diagnoses given do not clearly separate the Turrilinacea and the Buliminacea. Although defined as possessing simple aperture and toothplate the Turrilinacea include the Stainforthiidae with loop-shaped aperture and well developed toothplate. A triserial genus without toothplate is also given family status.

Within the Buliminacea the family Reussellidae is not well defined because the angular chambers are not mentioned. The distinction with the family Trimosinidae is not clear and this group probably deserves subfamily status only. Despite the difficulties experienced earlier with the Cassidulinacea the authors exclude hyaline-oblique forms from the Buliminacea and Turrilinacea and place them in the Fursenkoinacea. The family Fursenkoinidae can only be distinguished from the Stainforthiidae on this basis. I consider that the superfamilies Fursenkoinacea and Turrilinacea should be reunited in the Buliminacea, which should probably include the Delosinacea as well which shows development of septal pits and bridges like the Virgulinellidae. Similarly, I would include the Stilostomellacea (five genera only) in the Bolivinitacea on the grounds that they represent uniserial end forms. Note that Revets (1989), considers that *Buliminella* lacks a toothplate and should be excluded from the Buliminacea.

The superfamily Discorbacea is defined as low trochospiral but the first family within it, the Conorbinidae is defined as low to high trochospiral and it also includes, within the Eponididae, the subfamily Rectoeponidinae which becomes uncoiled and uniserial in the adult. The superfamily includes fifteen disparate families. No clear distinction is made between families such as the Discorbidae and Rosalinidae which have open umbilicus tending to become secondarily closed by umbilical flaps or bosses and those such as the Eponididae in which the umbilicus is primarily closed. I consider these features should carry more weight than the presence of the poreless patch used to bring together *Baggina* and *Cancris* which have very different umbilical characters. Poreless areas are common in genera of diverse groups and like ornament and surface texture should not be used at family level in isolation from other features. Incidentally, *Baggina* is defined as possessing closed umbilicus but on pl. 591, fig. 6, the umbilicus is shown to be open. The Discorbidae are described as having the chambers subdivided by a 'paries proximus' defined (Glossary) as a septal flap. This confuses the toothplate (umbilical flap) with the septal flap attached to the previous apertural face.

The superfamily Glabratellacea is distinguished from the Discorbacea by the presence of radial striae around the umbilicus on the ventral side which are presumed to facilitate and indicate plastogamic reproduction. The mode of reproduction in most foraminifera is unknown and it is difficult to accept that plastogamy and radial umbilical ornament is necessarily confined to one superfamily (largely to one family) considering the range of the morphologies (including the high trochoid *Buliminoides* considered *incertae familiae* by Revets (1989)) that are brought together by this approach. A case in point is that of *Rosalina parisiensis*. Specimens in the British Museum (Natural History) collections, ascribed to this species on grounds of prominent ventral ornament, include forms that otherwise clearly belong to *Discorbis*, *Rosalina*, *Discorbitura*, *Discorbinella*, *Neoglabratella*, *Neoconorbina*, etc. (Haynes and Whittaker in prep.). This suggests that ornament should be allowed little more than specific weight in this group.

The superfamily Siphoninacea is not adequately defined. The development of planispiral and streptospiral growth is only introduced in the definition of the family Siphoninidae. Uniserial should have been added to the description of the subfamily Siphonininae to distinguish them from the trochospiral to uncoiled, biserial Siphonidinae. However, there are only five genera in all.

The superfamily Discorbinellacea is distinguished from the Discorbacea on the basis of possession of an arched or slit-like equatorial, basal aperture but this superfamily definition is inadequate because genera with areal apertures such as *Discorbitura* are also included. This approach also brings together the Pseudoparrellidae, with closed ventral umbilicus and the Discorbinellidae with umbilical open or secondarily closed with umbilical flaps and/or bosses. It is also inaccurate in that four of the nine genera included in the family Discorbinellidae do not possess equatorial apertures. One of these genera, *Carlfranklinoides* is clearly shown to have radiating striae around the ventral umbilical aperture in pl. 631, fig. 14, although it is stated that 'none is present on the holotype'. On the authors' own criteria this genus should have been transferred to the Glabratellacea. The

genus *Cibicidoides* is transferred to the family Parrelloididae although the aperture appears to extend around the dorsal spiral suture as in other members of the *Cibicides* group. *Woodella* does not show the differentiation into a relatively poreless ventral side and coarsely perforate dorsal side given as a family characteristic, so all three genera placed here probably belong in different groups elsewhere.

As defined, the superfamily Planorbulinacea is stated to be distinguished by extra-umbilical to nearly equatorial aperture and coarse perforations while planispiral coiling is not mentioned. This would exclude the Planulinidae, trochospiral to planispiral and finely perforate with equatorial aperture, and the Cibicididae, aperture equatorial and possibly extending over the periphery and with a number of finely perforate genera. The Bisaccidae are irregularly planispiral with sutural canals so probably should, indeed, be excluded. Within the Cibicididae the genera are finely split but the distinctions are not clear, especially between *Cibicides* and *Lobatula*. *Discorbia* with umbilical flaps round an open ventral umbilicus would be better placed in the Discorbinellacea. The Planorbulinidae clearly derive from the Cibicididae but the Cymbaloporidae included here with them show no such relationship. The presence of umbilical apertures and cover plates, and lack of dorsal attachment surface indicates a closer relationship with the Discorbacea. *Montfortella*, included in the Cibicididae, should probably be transferred to the Victoriellidae which show the development of a pseudumbilicus with secondary umbilical openings on the spiral, ventral side. The range of the Planorbulinacea is given as Early Cretaceous to Recent on the basis of one genus only, *Epithemella*. Its ventral, umbilical aperture and attachment surface suggest removal to the Discorbacea. This would make the range of the superfamily, Late Cretaceous to Recent.

Spreading, irregular and branching forms are included in the superfamily Acervulinacea, described as lacking an aperture apart from mural pores. In *Acervulina* the aperture is stated to consist only of coarse perforations. However, the figures of *A. inhaerens* given on plate 659 clearly show peripheral and dorsal, sutural apertures resembling those of *Planorbulina*. This seems to indicate that *Acervulina* probably represents an extreme, irregular variant of *Planorbulina* and cannot be used as the type of a new superfamily.

The definition of the superfamily Asterigerinacea is inadequate in that it does not cover the orbitoidal Lepidocyclinidae which are included. It is also defective in that it includes the formation of supplementary chambers as a key feature which excludes the Epistomariidae, subfamily Nuttallidinae, on the authors' own criteria. Further, the families, Alfredinidae, Asterigerinatidae, Asterigerinidae (one genus only) and Amphisteginidae (one genus only) cannot be distinguished on the criteria given. The authors synonymize the Anomalinacea with the Asterigerinacea following the suggestion of Hansen and Rögl (1980) that *Anomalina* (Anomalinidae) is identical with *Epistomaroides* (Alfredinidae). Here the authors have acted hastily. The type of *Anomalina* has certainly been lost but the International Committee on Zoological Nomenclature has not yet suppressed the name. Although Hansen and Rögl recovered *Epistomaroides* from Mauritius but failed to recover the type species of *Anomalina* (*A. punctulata* d'Orbigny), in what is its type locality, this does not (and cannot) prove that d'Orbigny actually described what we now call *Epistomaroides* as *Anomalina*. This is unlikely because although there is a general similarity in coiling mode (shared by many genera) the apertural and sutural details are quite different. The case of *Anomalina* should remain open.

The superfamily Nonionacea is defined as 'planispiral to slightly asymmetrical' but a number of the genera included are described as low trochoid, such as *Spirotextina* and in the case of *Queraltina*, described as 'distinctly trochoid'. The *Pullenia* group is included in the family Nonionidae although they have primarily closed umbilicus and lack the distinct perforation of *Nonion* and its allies. *Melonis*, although it is described as having ten to twelve chambers in the final whorl, is included in the subfamily Pulleniinae, defined as possessing 'few chambers per whorl'. The Almaenidae are also included in this superfamily although the general form, peripheral apertures and coarse perforation suggest closer links with the Planorbulinacea.

The definition of the superfamily Chilostomellacea as trochoid and hyaline-oblique ('granular') is defective because the family Chilostomellidae is then defined as trochospiral to planispiral and hyaline-radial genera are included in the family Trichohyalidae. It also fails to cover the families included with the deep folds in the apertural face (Alabaminidae), supplementary apertures (Oridorsalidae) and toothplate (Coleitidae). Although the superfamily is defined as with ventral ('umbilical') aperture, the family Heterolepididae in which the aperture runs on to the dorsal side, as in *Cibicides*, is also included. This is largely because of wall structure, revealed by the authors' statement that 'optically granular' species of *Cibicidoides* should be transferred to *Gemellides*, a hang-over from their attempted splitting of the Anomalinidae on these grounds in 1964, shown to be unsound (Wood and Haynes 1957; Belleme 1974; Haynes 1981). This family is better included in the Planorbulinacea. The family Gavelinellidae differs from the Chilostomellidae in that the ventral aperture runs into the umbilicus which tends to become closed with umbilical flaps and is nearer to the Discorbacea. Genera with primarily closed umbilicus such as *Hollandina* and *Paralabamina* belong elsewhere. *Hanzawaia*, with flaps (lappets) on the dorsal side, is another anomalinid. *Discanomalina* as illustrated appears to include disparate forms and

requires restudy; the inclusion of Irene McCulloch's figures of *Pseudorosalinoides chatamensis* being possibly a *lapsus calami*. Unrelated forms also appear to be included in the family Trichohyalidae. *Trichohyalus* appears to be a highly ornamented discorbid, near to *Neoglabratella*, whereas *Aubignya* lacks radial costae and has umbilical lobes. The type of *Aubignya*, *A. mariei*, is closely similar to *Ammonia perlucida* and should probably be transferred to the Rotaliacea.

The treatment of the superfamily Orbitoidacea is confused. The family Orbitoididae is split into two subfamilies according to whether lateral chamberlets are differentiated or not but *Schlumbergeria* is synonymized with *Orbitoides*, although it is without lateral chamberlets and appears to be its undifferentiated ancestor. The superfamily is diagnosed as without canals and this is repeated in the definition of the family Lepidorbitoididae. However, the subfamily Lepidorbitoidinae is taken to include *Arnaudiella* which has radial canals. The subfamily is also taken to include the non-orbitoidal, canaliculate *Daviesina*, *Praesiderolites*, *Pseudosiderolites* and *Sulcoperculina*. These genera belong elsewhere but this treatment supports the idea of Van Gorsel that the Lepidorbitoididae originated from *Pseudosiderolites* (see Haynes 1981) and its inclusion in the Rotaliacea.

The superfamily Rotaliacea is inadequately defined because it does not cover the orbitoidal families. Pseudorbitoididae and Miogypsinidae which are included, or the conical Chapmaninidae. The Rotaliidae are defined as trochoid but include the subfamily Cuvillierininae defined as trochospiral to nearly planispiral. On examination this subfamily is found to include both trochoid forms, *Pseudowoodella* and fully planispiral forms, *Fissoelphidium*. These should be excluded, with the *Cuvillierina* group recognized as a full family. It is not clear what is meant by the distinction drawn between the subfamilies Rotaliinae and the Ammoniinae on the basis that the umbilical area is 'primarily closed' by an umbilical flap in *Rotalia*, while it is 'secondarily closed' by a foraminal plate in *Ammonia*. A scroll-like toothplate is attached below the areal foramen in *Ammonia*, whereas a partial umbilical partition is formed in *Rotalia* and the foramen remains a basal opening, like the primary aperture. Both appear to be built at the same time as the chamber. In both genera communication into the umbilical area below the umbilical ends of the chambers is initially open. In *Ammonia* the umbilical area tends to be filled with a plug or plugs. In *Rotalia*, the umbilical (astral) lobes coalesce and fuse as an umbilical coverplate similar to that in *Discorbis*. Together with the presence of the umbilical partitions ('toothplate') this prompted the suggestion by Lévy *et al.* (1984, 1986), that the Rotaliidae should be subsumed within the Discorbiidae. However, in the adult this coverplate is broken up by growth of pillars and development of open sutural canals by resorption (Haynes and Whittaker, in press) which clearly distinguish the genus from *Discorbis*. The authors also include the Elphidiidae, a primarily planispiral group in this superfamily. However, I believe a more natural place for this group is within the Nonionacea, as early forms grade with the Nonionidae both in wall structure and gross morphology. The appearance of the septal flap seems to have been an independent development in this superfamily (Haynes 1973).

The Nummulitacea are defined as planispiral but include the family Pellatispiridae described as planispiral to low trochoid. This family, without marginal cord and showing development of fissures, would more naturally find a place in the Rotaliacea. Incidentally, although the authors state 'vertical canals or fissures may be well developed', in the Pellatispiridae, they are not mentioned in any of the genera described, e.g. *Miscellanea*. The orbitoidal nummulitaceans are split into two families according to whether the annular chambers of the equatorial layer are divided or not. However, *Asterophragmina* is included in the Discocyclinidae, defined as subdivided, although the adult annular rings of this genus are clearly undivided (pl. 819), and in the genera included in the Asterocyclinidae, defined as undivided, the annular rings are clearly divided (Pls. 824 and 825). The reason for this apparent anomaly, is that the authors regard the annular rings of the Asterocyclinidae as consisting of cycles of small, spatulate to rectangular, primary chambers, whereas in the Discocyclinidae each adult equatorial chamber is a ring, that may or may not be subdivided into small secondary chamberlets. This should have been made clear. If it is actually the case, it indicates that these two families are of quite separate origin and probably belong to different superfamilies, other superfamilies in the scheme have been separated on features of rather less weight.

DISCUSSION AND CONCLUSIONS

Understandably, considering the complexity of the problem and the present state of knowledge, the authors have only been partially successful in producing a more natural (genetic) classification. Despite a brave attempt to 'untie the knot', they would almost certainly be the first to admit that large elements remain clearly artificial. Also, as pointed out by the reviewers, in many cases the diagnoses are vague and even contradictory and they have not been able to push through a

thorough-going, logical, hierarchical scheme. As might be expected, the large amount of new material and information that has become available (and is still in full flood) has produced more problems than it has solved. It has forced them to abandon their 1964 attempt to make a clearcut division on the basis of wall structure, aperture form and coiling mode and to raise other characters to suborder and superfamily rank. In so far as this is a measure of the real complexity of relationships it is to be welcomed, because there can be no return to past simplicities, however beguiling.

A positive attempt is made to solve the problem of Carpenter's perforate 'arenaceous' group by recognizing them as a separate superfamily. Although it is still not clear whether the diverse canaliculi, passages, pseudopores and tubuli in other agglutinated genera all represent separate lines, this move is supported by work on wall structure by Brönniman and Whittaker (1988) and by Bender (1989). Other changes, such as the use of surface texture at superfamily rank, are likely to be more controversial. Certain weaknesses also persist from their former classification. Despite the demonstration that hyaline-radial and hyaline-oblique ('granular') wall structure are close to each other, so that one is easily derived from the other, and the consequent abandonment of hyaline-oblique structure as a basis for recognition of the Cassidulinacea, this distinction is still a major factor in regrouping of genera in other superfamilies. The tendency to discount ontogeny as an indication of evolution is also inherited from the *Treatise* and also leads, I believe, to horizontal groupings, particularly in the case of the Textulariina and the Lagenina.

It is evident from this historical account, down to the latest and most ambitious attempt, that a stable, i.e. natural, classification of the Foraminifera is still a distant goal. The lesson for stratigraphers and, particularly, macro-evolutionists, is that they must treat suprageneric taxa and even genera with great caution. In the circumstances, workers not primarily interested in classification and evolution can be forgiven for thinking they should be abandoned. For instance, Culver *et al.* (1987, p. 169) suggest that, ideally, species-level data should be employed, because they doubt 'the significance of evolutionary generalisations based on the entirely human constructs of higher taxonomic categories'. But the horizontal limits we draw between species are also artificial, and as viewed in time, species are human artifacts, whether recognized as part of a phyletic line or as an allopatric branch (in both space and time) where the connecting cline is known. The objective biological reality of living species viewed as interbreeding population groups, separated from their closest relatives by morphological discontinuities, must not be confused with the subjective limits we are bound to draw between these species and their ancestors. For instance, even where we know the ancestry in a clear cut case of allopatric speciation, we still have the problem of deciding the limits between parent species (type subspecies), the peripheral subspecies (possible founder populations) and the new species (type subspecies). Most species are cryptogenes (the ancestry is not known) and we can only estimate the possible number of ancestral taxa and intermediate forms lost in the stratigraphical gaps or not preserved. We have to be careful not to confuse the species, as preserved, with the 'natural species' and appearance in the stratigraphical record with 'origination'.

It is precisely these confusions which vitiate recent attempts to replace 'traditional intuitive' taxonomy, by the methods of numerical taxonomy, or those of cladistics, with which it is hoped to draw hard and fast lines between species. In the case of numerical taxonomy, there will be no quarrel with the introduction of more refined measurements. It is the attempt to place reliance entirely upon numerical values, given equal weight, that cannot be sustained. Of course, if weighting is applied, the supposed 'objective' nature of the enterprise is destroyed. Numerical methodology cannot be more than the handmaid of taxonomy and in this role provides a very useful adjunct, as is shown by the work of Barnett (1974), Malmgren (1974) and Scott (1974).

In the case of cladistics we have to separate the extraordinary claims made for it as 'scientifically rigorous and operational' compared with traditional taxonomy, and its results in practice. Like numerical taxonomy, it pretends to objectivity in replying on morphological characters given equal weight to establish the degree of genetic difference. It is supposed that 'real' species, as distinct from 'hypothetical' species, can be defined on the basis of 'splitting events', i.e. 'discontinuities', and further, that these 'speciation events' are the only objective ('non-intuitive') boundaries, apart from

terminal extinction, available for definition of species taxa. Genera are taken to include daughter species and ancestral species back to the next available name.

The most ambitious attempt to apply cladistics to foraminifera is that by Fordham (1986), on the Cenozoic planktonic fauna of the Pacific, reviewed by Banner (1987), Chaproniere (1987) and Adams (1987). These authors are as one in dismissing it as neither objective, nor operational or practical. The discontinuities between species-clusters are distinguished by the first and last appearances of constituent subspecies (phenae), some by only one, although it is admitted they are arbitrary. The fossil record is presumed to be complete and no account is taken of discontinuities caused by variations in sedimentation rate, sedimentary breaks, oceanographical changes and inclusion in the death assemblage of species and subspecies adapted to different levels of the stratified water column. A further serious objection is that the method relies on a severely restricted model of allopatric speciation in which the dichotomous appearance of two daughter species leads to elimination of the ancestral species. As Adams points out, most biostratigraphical work proceeds on the 'well-justified' assumption that ancestral species do not necessarily die out as a consequence of speciation. Not only are geological events confused with originations of palaeontological species but also with biological 'speciation events'. Clearly, cladistics is a metaphysical system imposed upon the facts rather than arising from them. It is unlikely to lead to more soundly based species or supraspecific categories. The bold claim that 'Histories, terminations and the reproductive nexus are easy' (Kitcher 1989) will, therefore, ring hollowly in the ear of the practising taxonomist.

The central place occupied in cladistics by an extreme model of allopatric speciation reflects recent fashion, particularly in America (one does not have to be a marxist to see the connection). However, although Haldane (1959) prophesied that allopatric speciation would come to be accepted as the norm, and Ruse (1982) decided that 'totally sympatric speciation is rare', the stratigraphical record of the Foraminifera suggests that both rapid allopatric branching and relatively slower, sympatric transformation take place. Well known evolutionary trends in larger foraminifera interpreted as examples of phyletic evolution are shown by *Lepidolina* (Ozawa 1975), the *Orbitoides* lineage (Gorsel 1978), *Cyclocypus* (MacGillavry 1978) and in planktonics by the *Globorotalia menardii/tumida* lineage (Malmgren *et al.* 1983). The gradual trend in *Lepidolina* was dismissed as 'pseudogradualism' by Gould and Eldredge (1977) and a possible result of 'clone selection'. However, these larger foraminifera show both sexual and asexual generations.

One of the reasons for the popularity of exclusively, allopatric solutions may be that formerly, average selection pressure was thought to be quite low; Fisher (1930) considered 1% selection for advantageous qualities was a reasonable average throughout geological time. As a consequence, emphasis was put on the isolation of small populations (even reduction to a biblical pair) with only a fraction of the parental gene-pool, to account for rapid change. However, it is now known (Ford in Huxley 1974) that selective forces are up to thirty times greater in nature than had been realized, and therefore more effective on larger populations than previously admitted. After all, although the Galapagos finches are a remarkable example of rapid differentiation from small, immigrant, founder populations, the case of the medium ground finch (*Geospiza fortis*), which was permanently reduced to the large beaked form by a major drought (Boag and Grant 1981), represents rapid sympatric evolution through operation of an environmental 'bottleneck' on a relatively large population.

The many convergent lines of evolution towards complex orbitoidal structure in the large rotaliids appear to be related to the development of low fertility, reefal environments, perhaps with initial 'bottleneck' reduction to the most effective symbiotic species, amongst small rotaliids, followed by gradual acquisition of a more efficient algal-greenhouse structure. All the stages can be seen particularly well in the Miogypsinidae, Orbitoididae and Lepidocyclinidae. There is, of course, no occasion for the use of the 'morphological gap', but genera can be distinguished on the basis of important structural changes and innovations ('novelties' of Adams 1983), e.g. the appearance of lateral chamberlets which distinguish *Miogypsinina* from *Miogypsinoides*, and *Orbitoides* from *Schhumbergeria*.

Generic and suprageneric categories are natural as far as they represent clusters of species that

have evolved from ancestral groups by changes at the species (subspecies) level. Again, as far as they are natural, they will be 'real entities' that reflect major evolutionary responses to the challenge of global physiographic change and the opportunities provided by extinction of groups that formerly dominated a particular environmental range. Loeblich and Tappan's new classification, despite its imperfections, reveals even more dramatically than formerly how replacement has been a constant theme in the evolution of the Foraminifera (for ranges of the suprageneric groups see Ross and Haman 1989). Generic ranges are given by Danielle Decrouez (1989). However, it is sobering to realize that in no case is there direct proof of the evolutionary origin of any of the twelve suborders recognized and the ancestral groups remain speculative.

PRINCIPLES OF CLASSIFICATION

After the historical study it will be helpful to provide a brief statement of what appear to be the prerequisites of a more natural classification.

1. Foraminifera are the largest and most varied invertebrate group, have the most complex shells and include some of the largest protozoans. Although acellular, life histories are complex, there may be multinucleate phases and chromosome numbers are high. Even Class status may provide too narrow a framework for the complexity of relationships to be expressed.

2. A simple ordinal/subordinal scheme based on wall structure is not possible. There are at least two calcitic Palaeozoic groups, one microgranular, one largely 'vitreous'; both perforate and imperforate groups of agglutinated forms, plus a group secondarily derived from the miliolids; two groups of porcelaneous forms, one with perforate ancestry; four groups of microcrystalline calcitic, hyaline forms, the buliminids possibly derived from perforate agglutinated forms, the nodosariids from 'vitreous' ancestors, and the globigerinids and rotaliids of unknown origin. The relationship of the calcitic groups to the poorly known aragonitic group is obscure.

3. Coiling modes are not 'isomorphous' in the different wall structure groups but adaptive radiation at different times into broadly similar environments and ecological niches has led to heterochronous homoeomorphy with the constant repetition of certain styles. There are trends in test architecture towards both increased complexity and simplification and both coiling-up and uncoiling (even recoiling and uncoiling) occur. In general, groups adapted to vagrant surface feeding in high energy environments remain close-coiled; groups secondarily adapted to infaunal environments often show uncoiling and simplification with growth and attendant serial, apertural modifications; groups adapted to symbiotic life show increased size and complication of structure. Contrasting modes within the larger Foraminifera illustrate the 'developmental constraints' of the non-lamellar test, i.e. only the *Somalina* line in the porcelaneous group achieves 'orbitoidal' structure. New features tend to occur in the adult and proterogenesis is less common, but especially in symbiotic forms there is often striking differentiation of the juvenile (possibly connected with dispersal). Multiform genera probably adopt different life habits at different stages. Neotony may be a factor in the rise of certain groups, such as the planktonics. Ontogeny, therefore, has to be used with great care as a guide to phylogeny.

4. Only detailed stratigraphical and evolutionary studies can solve the problems of iterative evolution, parallel development and convergence peculiar to Foraminifera. In these circumstances, numerical taxonomy and cladistics (which in its 'transformed' manifestation excludes these problems from consideration) cannot be substituted for traditional taxonomy, i.e. the careful comparison of test architecture and wall structure, apertural and internal features, taking gross similarities and differences into account, with the evidence of ontogeny and the stratigraphical record, to establish phylogeny.

5. Although it is not true that traditional taxonomy relies exclusively on unique rather than shared characters, as supposed by Fortey (1989), care must be taken not to employ any one feature as a single 'key'. As Carpenter put it, 'a natural system depends on the whole aggregate of ascertainable characters'. In this aggregate we must include coiling-mode; banished by Carpenter but continuing to haunt classification like Banquo's ghost. The supposition that features established

at one level in one order can be applied with equal weight in another order, with a different evolutionary history, must also be avoided.

6. 'Species are made by isolation,' as Darwin put it, but populations can be 'islanded' in time as well as space and evolutionary patterns are complex in Foraminifera, suggesting that both allopatric branching and sympatric phylogenesis have taken place. As is to be expected, rates are variable, though sympatric phylogenesis appears generally to be relatively slow, perhaps because selection is working on larger populations. Attempts to arrive at an 'objective', supraspecific classification by application of a stereotyped model of dichotomous allopatric speciation should be avoided. Darwin's famous model of the irregularly branching tree of life (the only diagram in the *Origin*) is more appropriate. Also, as pointed out by Adams (1983) the relatively rapid appearance of 'novelties' which then become stable, together with the slower modification of existing characters can give the appearance of punctuated equilibrium and gradualistic evolution in the same family.

7. The contribution of biological studies, although important, is so far limited. Paradoxically, despite their stratigraphical importance, less is known about living Foraminifera than about the living representatives of any other major group. Further studies of life history, functional morphology, genetics and cytology are a *sine qua non* of an improved classification. The study of living, naked forms (Allogromiida) is also a particular need.

Acknowledgements. I am indebted to the two referees who commented on the original draft of this paper, intended as an essay review of Loeblich and Tappan's book, and who encouraged me to examine it in historical context, especially in regard to problems that can be traced back to the work of the English School. In particular, Dr C. G. Adams and Dr J. E. Whittaker provided references and copies of reviews of earlier classifications, including the attempt to use cladistics by Fordham. Unfortunately, I was unable to borrow a copy of the doctoral thesis on foraminiferal classification by Martin Janal for copyright reasons. The paper was typed by Mrs Janice Evans.

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Typescript received 5 April 1989

Revised typescript received 4 December 1989

NOTE ADDED IN PROOF

Since the publication of Loeblich and Tappan's book in 1988 the following modifications have been made to their subordinal scheme. First, Loeblich and Tappan (1989) have recognized the new suborder Trochamminina of Brönniman and Whittaker (1988) and in addition they have reinstated the suborders Haplophragmiina and Astrorhizina. This gives the following four-fold breakdown for the agglutinated group:

- Astrorhizina – unilocular with organic cement
- Trochamminina – multilocular, cement organic, wall simple
- Haplophragmiina – multilocular, cement organic wall simple to alveolar
- Textularina – multilocular, cement calcareous, typically canaliculate

Secondly, Revets (1989) has erected the new suborder Delosinina to accommodate the genus *Delosina*, considered to have a unique monolamellar, irregular microgranular, calcitic wall. The addition of this last would bring the number of suborders in Loeblich and Tappan's scheme to sixteen.

Further to the above it can now also be stated that the International Committee on Zoological Nomenclature has decided to take no action in the case of *Anomalina* and the Anomalinidae and their status therefore remains unchanged (Whittaker, pers. comm.).

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ONTOGENY, HYPOSTOME ATTACHMENT AND TRILOBITE CLASSIFICATION

by R. A. FORTEY

ABSTRACT. The high level classification of trilobites has proved particularly difficult. This paper discusses the classification of those trilobites which have been placed in the Order Ptychopariida, together with other relevant groups, including Agnostida. Although often considered 'generalized', the ptychoparioids have a distinctive derived character: the hypostome is not exoskeletally connected to the cephalic doublure (natant hypostomal condition). The polarity of the natant hypostome as a derived character is supported both by known ontogenies, and by comparison with other trilobites, and is unusual in primitive arthropods as a whole. The wide distribution within the Trilobita of the natant hypostomal condition is established. The primitive state, found in redlichiids, is conterminant, in which the hypostome is attached to the cephalic doublure and closely corresponds ventrally with the frontal glabella lobe. Several trilobite groups which primitively had natant hypostomal condition became secondarily conterminant, e.g. among Asaphida and Proetida. All trilobites having natant hypostomal condition, together with those which were primitively natant and only secondarily conterminant or impendent, are believed to constitute a new monophyletic group termed the Subclass Libristoma. This group includes the majority of the trilobites. A number of major monophyletic groups within the Libristoma are recognized, and one or more autapomorphy for each group is described. The Ptychopariida can be reduced in scope to a paraphyletic group of primitive libristomates which cannot yet be assigned to a clade. The other major groups of Libristoma include: Asaphida, Proetida, Olenina, Harpina. There is slim evidence that the Phacopida also had libristomate ancestry. Some groups included in Ptychopariida in the 1959 *Treatise* can now be assigned to different higher taxa. Illaenacea (= Scutelluina) and Leiostegiacea probably belong within a large corynexochoid clade; Damesellacea are regarded as the primitive sister group of Odontopleurida. Agnostida are not libristomates, but they *are* trilobites; they are more advanced than olenellids, and comprise the sister taxon of Redlichiida + all other trilobites. An important autapomorphy defining Agnostida is the loss of calcification of an olenelloid-like rostral plate.

Natant hypostomes are conservative in morphology, and it is often difficult to assign the hypostome among natant families. Specialized hypostomes are associated with the conterminant or impendent hypostomal condition. The natant condition is lost polyphyletically, and there is some evidence that secondarily conterminant trilobites arose when primarily conterminant groups became extinct. The relationships of subgroups within the Libristoma, and the relationships of other major conterminant taxa (corynexochoids, Odontopleurida, Lichida, Phacopida) to one another and to the Libristoma remain to be explored before the taxonomic status of major groups can be decided. The Redlichiida is probably another paraphyletic group having the same relationship to all higher trilobites as does the Ptychopariida within the Libristoma.

TRILOBITES are one of the most morphologically diverse invertebrate groups with a good fossil record. Their long stratigraphical history and abundance has meant that students of the group have specialized in faunas of a particular age, or upon particular groups. It is possible to spend a productive working life studying one or two families through one or two systems, and no single worker has a detailed knowledge of the whole Class. Most specialists are concerned with classification and relationships of trilobites at subfamily, genus or species level, for which there is now an overwhelming literature. There is no uniformity of taxonomic usage throughout the group, and it is probably true that taxonomic practice tends to change, with the specialists, at system boundaries. Cambrian workers tend to be much more influenced by palaeogeography and stratigraphy than are Ordovician specialists; Devonian and Carboniferous workers tend to employ more taxonomic categories (subgenera and subspecies) than do workers lower in the column. Generally these disparities in approach cause little difficulty. However, a more important

consequence of specialization concerns classification at the taxonomic level above the family, and the relationships *between* families. Changeover between families often coincides with stratigraphical boundaries, and falls between the provinces of different specialists. The latter may take the higher categories as 'given' and concentrate instead upon the kind of within-group evolution that can be revealed by detailed stratigraphic studies. The problem is compounded by the fact that families often appear to be good, clear categories, with distinctive autapomorphies characterizing them, but the synapomorphies which can relate one family to another are far less clear. Nor have stratigraphical 'transformation series' of species connecting one higher taxonomic category with another been discovered in many cases – the families appear, as it were, ready made. Many of these natural groups were recognized already by Salter (1864, p. 2). No trilobite taxon is more intractable than the Order Ptychopariida with regard to the groups that should, or should not be included within it. Nor is it clear from the literature whether the Ptychopariida is a natural group. This paper is an attempt to approach some of these problems by discussing characters which are of service in characterizing ptychoparioid trilobites. In this endeavour I am acutely aware of the limits of my own detailed knowledge, particularly of Cambrian trilobites. But new insights into high-level classification are needed before the publication of the revision of the volume on trilobites of the *Treatise on invertebrate paleontology*.

HIGH LEVEL TRILOBITE CLASSIFICATION

The few trilobite workers who have attempted to discuss higher level trilobite classification, for example, Stubblefield (1936), Henningsmoen (1951), Harrington (*in* Moore 1959), Bergström (1973) and Fortey and Owens (1975), have stressed the need for a natural classification, by which is meant a classification that reflects phylogeny. Even so, it is apparent that higher level taxa claimed 'natural' by one worker may be disputed by another – see, for example, Bergström's (1977) discussion of Fortey and Owens' (1975) Order Proetida, and Fortey and Owens' (1979) reply. In dispute in such discussions is the meaning of particular characters: the claimed synapomorphies of one authority are disputed as homoplasies by another. Trilobites are not simple subjects for phylogenetic analysis. Cladistic analyses of character distributions offer a new approach to the problems of classification. A pioneering attempt in this direction was made by Eldredge (1977). But the cladogram he produced was based on few characters, was replete with unresolved polychotomies, and many of the groups indicated would now be in dispute. Eldredge admitted that his analysis was not satisfactory, referring to 'the chaotic and rudimentary state of our understanding of trilobite relationships' (p. 326). A very detailed account of one group, the Suborder Asaphina, which included a cladistic analysis based on a large matrix of characters, was published by Fortey and Chatterton (1988). This analysis depended on the recognition of at least one character (the ventral median suture) which served to define the whole asaphine group. Although reasons were advanced why this character was likely to be a good synapomorphy there may be workers who disagree (i.e. who claim that the median suture was polyphyletically derived). Higher Asaphina also have a distinctive kind of protaspis, and this, too, was regarded as important in recognizing the relationships of some very disparate adults. The foundation of Fortey and Chatterton's analysis was the recognition of at least one apomorphic character uniting the Asaphina.

Cladistic classifications also attempt to resolve taxonomic units into monophyletic groups (Wiley 1981). In this respect they may part company with more traditional approaches used by trilobite taxonomists in which the status of a higher taxonomic unit may be determined by some assessment of its morphological difference compared with other trilobites, rather than its common ancestry. The formal recognition of paraphyletic groups (that is, groups descended from a common ancestor, but not including all its descendants) is also common practice in existing classifications. The writer regards the definition of groups by common ancestry as a desirable goal in producing a classification which is truly 'natural'. This is not the place to develop the theoretical basis for this approach, but I broadly follow the reasoning set out previously (Fortey and Chatterton 1988) and by such authors as Jefferies (1986). However, for reasons which will become clear below, it is not always possible,

even if it is desirable, to eliminate paraphyletic taxa completely from groups with a good fossil record.

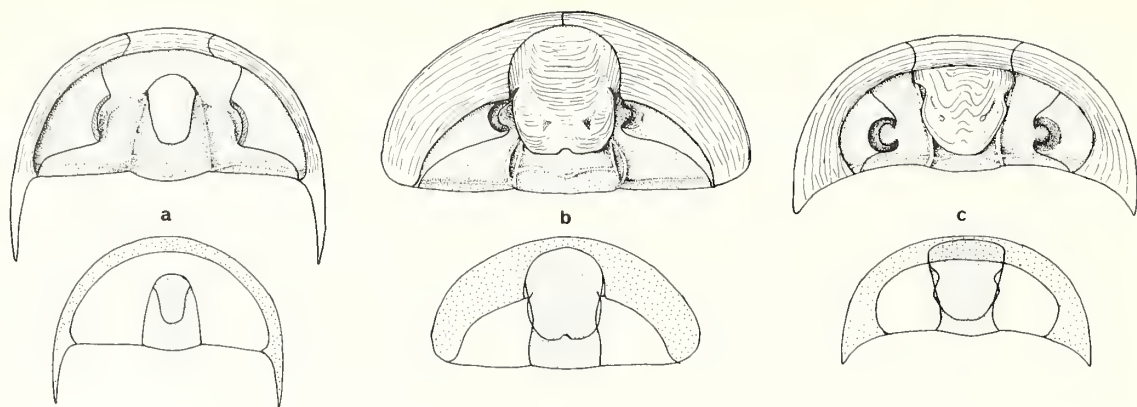
When Fortey and Chatterton (1988) treated the Asaphina, they left aside the question of the relationships of that suborder within the more inclusive Order Ptychopariida. In the *Treatise* (Moore 1959) the Ptychopariida occupies well over half the systematic section – as conceived there it is a vast assemblage of trilobites. Bergström (1973) reduced its scope, largely by elevating previous subgroups of Ptychopariida into separate orders. Of the relationships between these orders there was little discussion. Moreover, even the constituent families of Asaphina *sensu* Fortey and Chatterton (1988) were distributed among three different orders and several different suborders in Bergström's tabular classification. Nor were the characters on which the classification was based discussed in a way which is helpful for a phylogenetic classification. For these reasons a more inclusive view of Ptychopariida is the one adopted here.

The purpose of this paper is to investigate the problems in a phylogenetic definition of 'ptychoparioid' trilobites: do they constitute a monophyletic group, and if so which higher taxa may be eligible for inclusion within it? I employ the informal term 'ptychoparioid' for all the trilobites that have been considered in this context. My original intention was to tackle the problem using a computer-based cladistic analysis of probable constituent taxa, based on as many characters as possible. However, the characters that appear to be important as potential synapomorphies have either not been recognized, or not discussed in a phylogenetic context, and it is necessary to make a start by examining these characters. It is the characters which define the scope of the problem by indicating which taxa should be included in any more detailed review in the future. Although this paper concerns trilobites which have been regarded, or might prove to be Ptychopariida, it is hardly possible to avoid mentioning some of the other trilobite orders (Redlichiida, Phacopida, Corynexochida, etc.). There are problems in these groups also, but to keep the discussion within sensible bounds the discussion of such problems is briefer than it should be.

A sceptic might contend that, given the difficulties in producing a satisfactory high level trilobite classification, it might be better to adopt the 1959 *Treatise* classification (Harrington *in* Moore 1959) as a convention and forego attempts to produce a phylogenetic classification, or, like Zhang and Jell (1987), abandon all categories above family. One could at least 'pigeon hole' trilobites in this case. Such a view would quickly become self-defeating because there would be no criteria to decide the status (family? genus? superfamily?) of the various groups, and would result in a proliferation of names as more trilobites with intermediate combinations of characters were discovered. Also, broader palaeobiological theories which may be of interest to the non-specialist require a taxonomic base of 'natural' units. To cite one example, extinction patterns are a current concern, but if the 'extinction' is merely one of the disappearance of an arbitrary unit at a boundary between separate specialists it becomes meaningless (a 'taxonomic pseudoextinction' in the usage of Briggs *et al.* 1988). Conversely, it is of some interest that the extinction event at the Ordovician-Silurian boundary affects the suborder Asaphina more than any other group – a fact that was not known until the Asaphina were phylogenetically defined. I firmly believe that the recognition of natural groups is a priority in trilobite classification, even if the process is likely to prove contentious.

HYPOSTOME ATTACHMENT CONDITIONS

Fortey and Chatterton (1988, text-fig. 5) briefly introduced three terms to describe the relationship of the hypostome to the cephalic doublure on the venter, and the glabella on the dorsal surface (text-fig. 1). This character is of importance to the arguments in this paper. Whittington (1988*a, b*) has provided timely reviews of hypostomal attachment in the trilobites. He claimed that the anterior wings of the hypostome correspond with and were connected to the anterior pits in the glabellar axial furrows (or, if the pits are not clearly developed, to the appropriate point in the axial furrows); these structures are homologous in all trilobites. There are some differences in terminology between Whittington (1988*a, b*) and Fortey and Chatterton (1988) but only minor discrepancies in

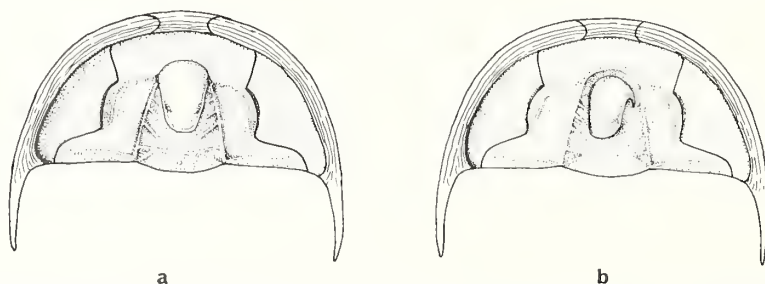


TEXT-FIG. 1. The three conditions of hypostome attachment illustrated by cephalic shields viewed from the underside. The explanatory cartoons below show cephalic doublure as coarse stipple, the outline of the glabella in fine stipple, and the hypostomal outline transparent to make clear the relationship between the hypostomal anterior margin and the preglabellar furrow. *a*, natant hypostomal condition, with 'detached' hypostome, illustrated by *Elrathia kingi*, Middle Cambrian, $\times 5$; *b*, conterminant hypostomal condition, hypostome attached and closely correspondent with glabella outline, illustrated by *Gog catillus*, early Ordovician (after Fortey 1975), $\times 1$; *c*, impendent hypostomal condition, with no close relationship between anterior margin of glabella and that of the hypostome (see also text-fig. 5a-c), *Raymondaspis reticulata*, mid Ordovician (after Whittington 1965), $\times 3$.

interpretation. However, a greater emphasis is placed here on the relationships of the hypostome to other dorsal structures.

Natant hypostomal condition

This term (text-fig. 1a) was applied by Fortey and Chatterton (1988) to those trilobites in which the hypostome was not attached to the cephalic doublure, but lay beneath the front of the glabella, separated from the doublure by a gap. Whittington (1988a) used the term 'detached' to describe the same condition. Because of this absence of firm connection it is unusual to find trilobites with natant hypostomal condition with the hypostome in place. One relies upon individuals that died on their backs, the hypostome falling down into the forward part of the glabella (Rasetti 1952a) upon the decay of the soft tissue (text-fig. 2). Despite this, hypostomes of a wide range of families are known or inferred to have had natant hypostomal condition, as listed below. The existence of the same hypostomal condition can be inferred for many more trilobites of which complete remains are unknown. This is when the genal doublure (or by extension the rostral plate) corresponded in width



TEXT-FIG. 2. Natant hypostome in life position (*a*), and as it falls down into the glabella on death in those trilobites which died on their backs (*b*) illustrated by generalized ptychoparioid. Compare with Plate 1. Note how glabellar furrows occupy area to each side of the hypostome.

with the marginal rim (Pl. 1, fig. 2). If the marginal rim was separated from the front of the glabella by a preglabellar field, and given that the hypostome lay beneath the frontal part of the glabella (in the position consistent with the anterior wing/anterior pit correspondance), then the hypostomal condition was natant.

Those hypostomes which were not natant were rigidly attached to the cephalic doublure (Whittington 1988a, b). It is more difficult to assess the degree to which the natant hypostome was fixed in place by the anterior hypostomal wings. The fact that the hypostomes in life position are so readily displaced implies that the connection was not likely to have been particularly rigid. Also I have seen numerous examples of entire cephalic shields which should retain a natant hypostome, but of which there is now no trace (Pl. 1, fig. 2), implying that it was easily separated. Dr R. M. Owens informs me (pers. comm. 1987) that of the many proetide exoskeletons he has studied with natant hypostomal condition when the hypostome is found at all it is invariably slumped to one side in the forward part of the glabella, in the manner of text-fig. 2b, implying that its support was not rigid (a similar conclusion was reached by Whittington and Campbell 1967). For these reasons it is likely that the connection between anterior wings and anterior fossulae was ligamental, and that, in life, there was probably a degree of freedom for movement of the hypostome. For example, up and down movement of the adoral margin might have been possible by means of muscles attached to the middle furrows on the hypostomal middle body, using the ligamental attachment of the anterior wings as 'rockers'.

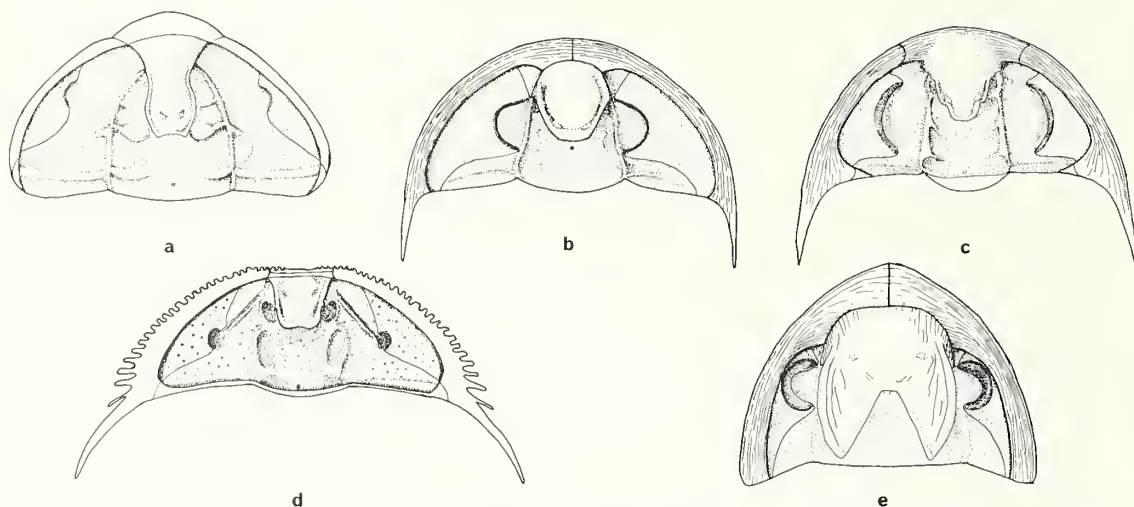
Natant (swimming) is an appropriate term to describe this hypostomal condition, even though the labral plate was probably tethered or anchored in at least some cases rather than truly free-lying and supported only by the ventral membrane. But some ptychoparioid hypostomes have such reduced anterior wings (e.g. *Bienvillia tetragonalis broeggeri*, see Henningsmoen 1957, pl. 11, fig. 7) that it is possible to be sceptical whether they were attached at all. The term natant is preferred to Whittington's 'detached' for two reasons: (a) 'detached' has a vernacular use which can apply to fortuitously separated hypostomes with other kinds of attachment modes; (b) if the natant hypostome is homologous in various trilobites, and is an unusual character in arthropods as a whole (below) then it requires a diagnostic epithet to describe it. Note that there is no direct connection between a trilobite having natant hypostomal condition and the configuration of the ventral sutures, so that natant hypostomes can be found with rostral plate (Ptychopariacea), median suture (e.g. Pterocephaliidae) or fused cheeks (most Olenidae).

Orientation. The connection between hypostomal anterior wings and anterior fossulae or pits in the axial furrows (Whittington 1988a) positions the hypostome in a way which corresponds with the anterior part of the glabella on the dorsal surface. This conforms with the position in which 'in place' natant hypostomes are found (see text-fig. 2 and Pl. 1). The anterior pits are in the axial furrows in front of the eye ridges, which in ptychoparioids are directed towards the anterolateral corners of the glabella. Because the anterior outline of the hypostome curves forwards, in the life orientation this profile approximates closely to the front glabellar margin, i.e. the outline of the preglabellar furrow. *The outline of the anterior margin of the hypostome closely corresponds with that of the glabella, and lies a short distance ventrally below it.* If Whittington's view of the upward projection of the anterior wings is correct (e.g. Pl. 1, fig. 5) there are some forms in which the front margin of the hypostome cannot have been far removed from the preglabellar furrow. The close correspondence dorso-ventrally between hypostome and glabella is an important point because it is retained in all trilobites except those in which the hypostomal condition is impendent.

With the hypostome restored in this position, in the typical ptychoparioid (*Ptychoparia*, *Elrathia* and the like) it is probable that the distribution of the glabellar furrows is related to the position of the hypostome (text-fig. 2a). The longest, posterior 1S furrows are posterior to the hypostome; the progressively shorter three anterior pairs of furrows occupy the gap between the hypostome and the edge of the glabella.

Conterminant hypostomal condition

In the conterminant hypostomal condition (text-figs. 1*b*, 3) the hypostome is in the same relative position with regard to the glabella as in the natant condition, i.e. the front margin of the hypostome and that of the glabella closely correspond. However, the hypostome is suturally joined to the inner edge of the doublure, and in all the described cases (Fortey and Chatterton 1988; Whittington 1988*a*, *b*) this attachment was rigid. Even in the absence of articulated material the conterminant



TEXT-FIG. 3. Conterminant hypostomal condition of various types, illustrated by ventral views of cephalic shields with hypostomes in place. *a*, the primitive calymenid *Neseuretus* (early Ordovician), in which conterminant condition is maintained by a broad anterior flange on the hypostome (mostly after Henry 1980), $\times 2$; *b*, secondary conterminant hypostomal condition with backward curvature of doublure in *Proceratopyge* (Asaphida; Ceratopygidae: late Cambrian; after Jago, 1987), $\times 3$; *c*, primary conterminant hypostomal condition in which rostral plate and hypostome are fused together as a single unit in *Fieldaspis* (Corynexochida: mid Cambrian; mostly after Whittington 1988*a*) $\times 3$; *d*, primary conterminant hypostomal condition with narrow, transverse rostral plate, in the odontopleurid *Leonaspis* (Silurian; after Chatterton and Perry 1983), $\times 8$; *e*, secondary conterminant hypostomal condition with hypostome recessed in doublure and occupying large part of venter, *Isotelus* (Asaphidae: middle Ordovician) $\times 1$.

EXPLANATION OF PLATE I

Natant hypostomal condition, including entire exoskeletons with hypostome more-or-less in life position (see text-fig. 2).

Figs. 1, 5. Olenidae: *Hypermeaspis*. 1, dorsal exoskeleton lying on its back within nodule, early Ordovician, Bolivia, USNM 380856, $\times 1.5$. 5, hypostome from lateral view to show upward-directed anterior wings, early Ordovician, Spitsbergen, Sedgwick Museum (SM) A84079 (see also Fortey 1974, pl. 14, fig. 10), $\times 4$.

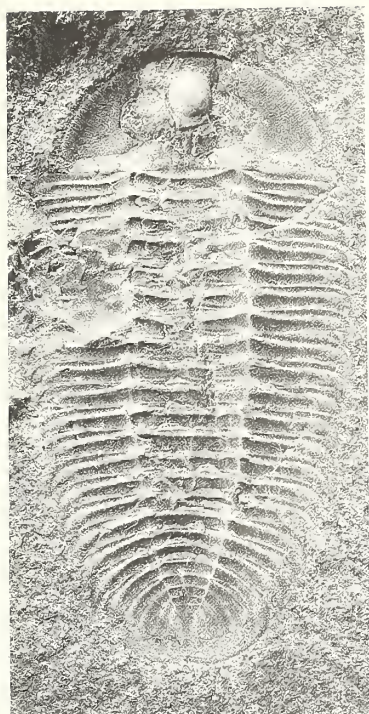
Figs. 2, 8. Asaphiscidae: *Blainia*, two exoskeletons from same block, mid Cambrian, Alabama, USNM 62801, one showing narrow (sag.) rostral plate but lacking hypostome, the other showing hypostome in usual position in natant forms, $\times 4$.

Fig. 3. Cedariinae: *Cedaria*, showing rostral plate and position of hypostome, U. Cambrian, Utah, USNM 300, $\times 4$.

Fig. 4. late olenid hypostome, *Balnibarbi*, early Ordovician, Spitsbergen, SM A84021, $\times 5$.

Fig. 6. Alokistocaridae: *Elrathia*, mid Cambrian, Utah, preserved dorsal side up but clearly showing rostral plate and position of hypostome, BM (NH) It 1734, $\times 2$.

Fig. 7. Proetidae: *Proetus*, Silurian, Wenlock, SM A28263 (Owens 1973, pl. 3, fig. 9), $\times 5$.



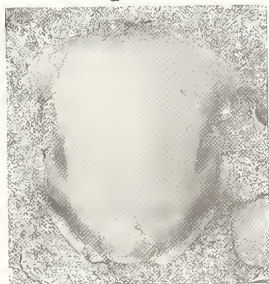
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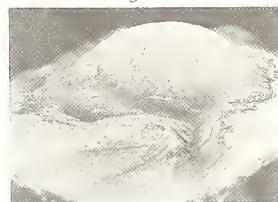
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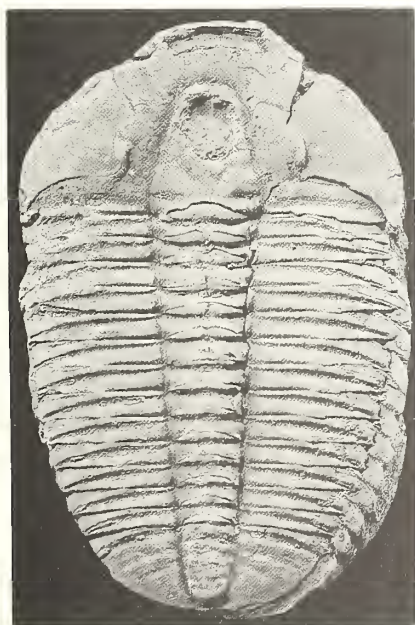
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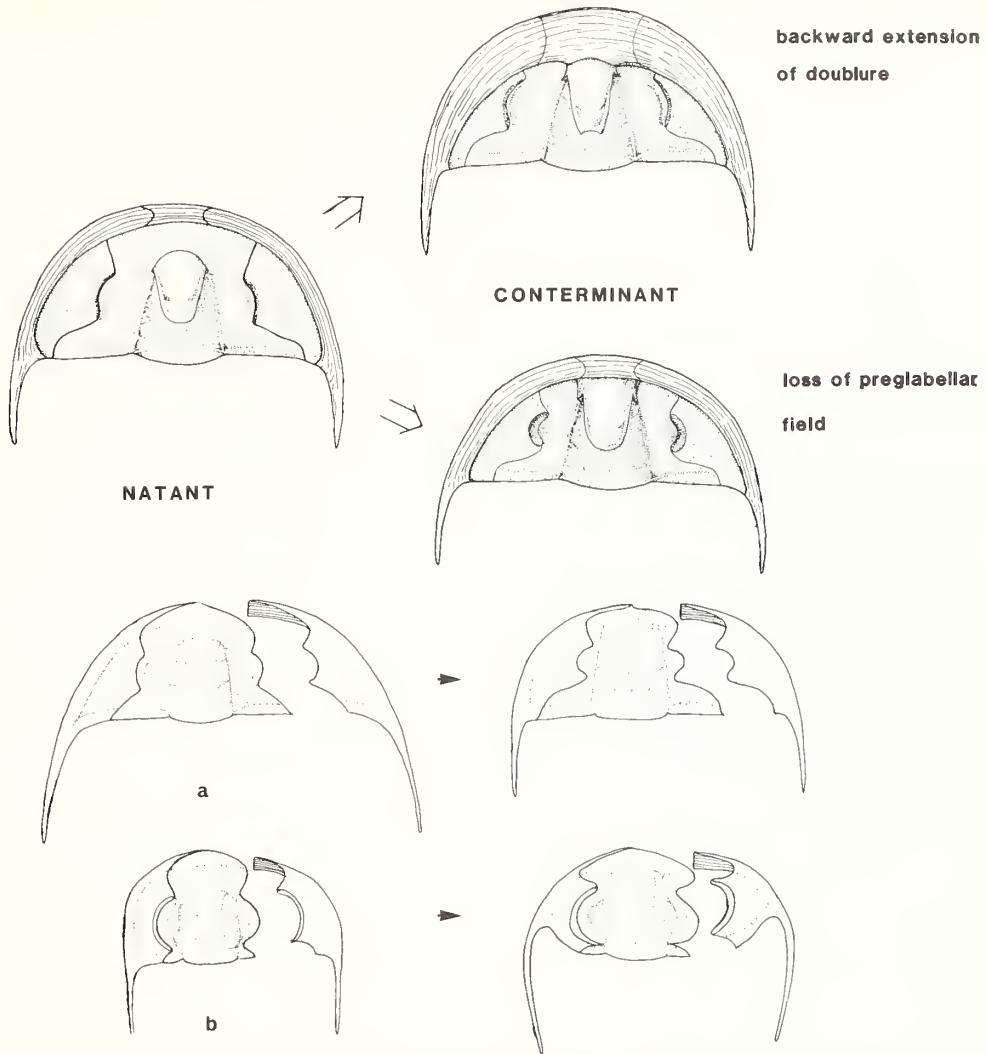
FORTEY, natant hypostomes

hypostomal condition can be inferred if the inner margin of the doublure extends as far as the front of the glabella, but no further (text-fig. 1*b*). Conterminant hypostomal condition can be found in trilobites with rostral plate, median suture, or with the cheeks conjoined ventrally. The hypostomal suture may become obsolete in trilobites with conterminant hypostomal condition, so that the hypostome and rostral plate form a single unit, as in *Corynexochida* (text-fig. 3*c*) and some *Paradoxididae*. Conterminant hypostomal condition is found in numerous trilobite families, of which several examples were described by Whittington (1988*a, b*) or by Fortey and Chatterton (1988): *Dalmanitidae*, *Asaphidae*, *Remopleuridae*, *Ceratopygidae*, *Cheiruridae*, *Calymenidae*, *Corynexochidae*, *Lichidae*, *Odontopleuridae*, *Encrinuridae*.

1. *Secondary conterminant hypostomal condition.* Conterminant hypostomal condition may develop secondarily from the natant condition. This is shown by examples within accepted monophyletic groups: *Anomocaridae-Asaphacea*; *Remopleuridacea* and *Proetida*. This secondary development is proved from stratigraphic evidence which shows that early and primitive members of the group are natant, and that later, more derived members are conterminant; and from comparison with the respective out-groups, in which the natant condition also pertains. These examples are important because they show: (a) that the conterminant condition is certainly not primitive for some *Trilobita*, and (b) that the conterminant condition can be attained from the natant by two different mechanisms (text-fig. 4). There is no known case where the conterminant condition returns to the natant condition – and hence it becomes a good derived character in classification.

Anomocaridae-Asaphacea. The relationships between the families included in the *Asaphacea* were reviewed by Fortey and Chatterton (1988). Most *Asaphacea*, in which Fortey and Chatterton included *Ceratopygidae* as well as *Asaphidae*, had a conterminant hypostomal condition. The primitive sister group, which probably included the common ancestor of both families, was the paraphyletic group *Anomocaridae*. *Anomocarids* certainly included some genera, such as *Anomocarioides*, which had natant hypostomal condition, the inner margin of the cephalic doublure falling well short of the front of the glabella. In fact, Fortey and Chatterton could find no member of the *Anomocaracea* which was convincingly conterminant. However, some species placed within this group had relatively wide cephalic doublure, so that the 'gap' between its anteromedian margin and the front of the hypostome was reduced. In early *Ceratopygidae* (*Proceratopyge* spp.) it was shown that the hypostome was attached to the doublure, and this was achieved by a median widening of the doublure (Jago 1987). This widening was indicated on the dorsal surface by adaxial backward curvature of the paradoublural line(s). In *Asaphidae* the doublure is wide both beneath free cheeks, and under the (usually wide) preglabellar area, before terminating on a line coincident with the preglabellar furrow (text-fig. 1*b*). The relatively great width of the cephalic doublure possible in this group suggests that the preglabellar field was 'lost' by backward extension of the doublure beyond the marginal rim at which it terminated in the *ptychoparioids*. In some conterminant asaphids doublure and frontal area are again narrow, but stratigraphic evidence suggests that this narrowness may be secondary. In any case the anomocarid-asaphacean transition (text-fig. 4*a*) involves secondary docking of the hypostome with the doublure – which may become very wide in the process – and attendant loss of the natant hypostomal condition. A few advanced asaphaceans attain the independent hypostomal condition.

Remopleuridacea and Dikelocephalacea. These two superfamilies were regarded as closely related within the *Asaphina* by Fortey and Chatterton (1988), and *Dikelocephalacea* is used in the sense of Ludvigsen and Westrop (1983) to include *Ptychaspidae* of authors. Early *Remopleuridacea*, such as *kainellids* and *Elkanaspis* Ludvigsen, 1982 have a narrow marginal cephalic rim, and the doublure ventrally corresponds with the rim. Species having a wide preglabellar field are therefore likely to have had natant hypostomal condition (Fortey and Chatterton 1988, text-fig. 14). In later and more advanced *Remopleuridacea*, especially *Apatokephalus* and its allies, the glabella extends forwards as far as the border, and the width of the cephalic doublure medially (e.g. Ross 1951, pl.



TEXT-FIG. 4. Two possible mechanisms (above) for attaining secondary conterminant hypostomal condition from natant hypostomal condition illustrated by generalized ptychoparioid of elrathiid type. Two examples (below) of secondary conterminant condition, primitive natant morphology to left and position of hypostome shown as dotted outline: *a*, anomocaracean *Litocephalus* (after Palmer 1960) (left) and primitive asaphid *Promegalaspides* (right); *b*, remopleuridaceans *Elkanaspis* (left) and *Menoparia* (right) (after Fortey and Chatterton 1988).

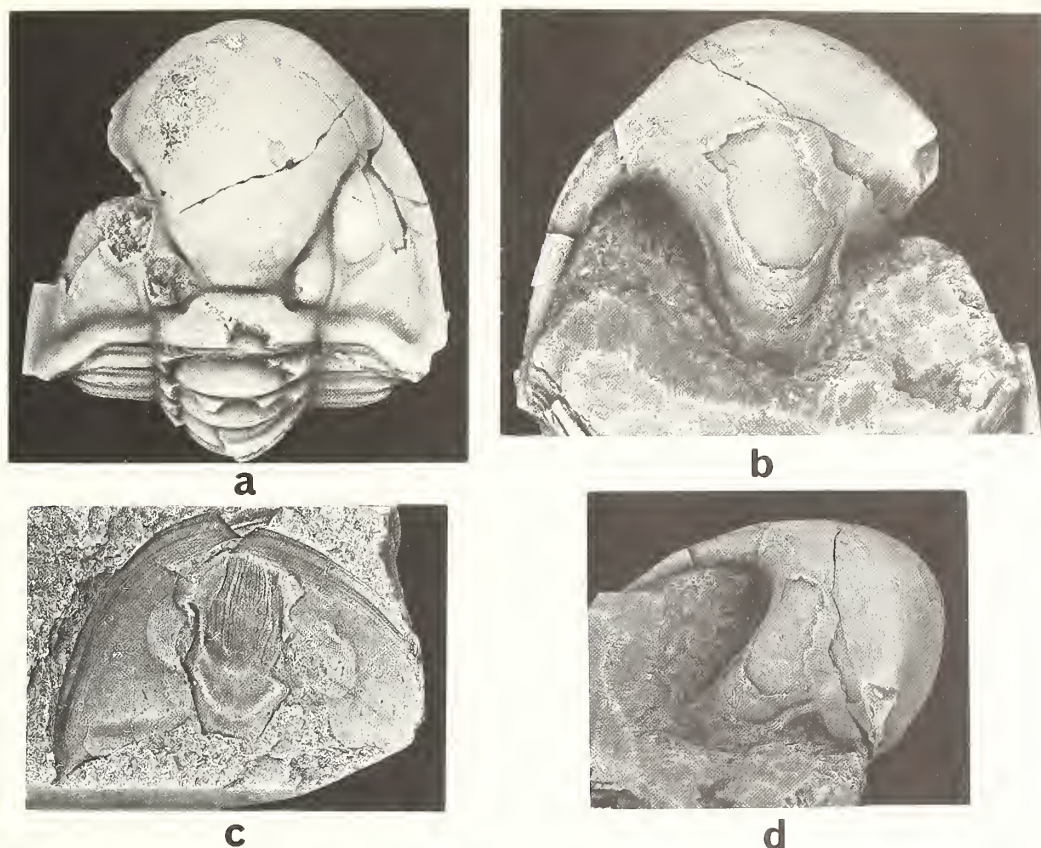
20, fig. 30) indicates that the hypostome had docked at this stage to become conterminant (text-fig. 4b). In the most advanced members of the family Remopleurididae the glabella has encroached forwards still further so that the hypostomal condition becomes impendent, and the rigid hypostomal attachment of such forms has been familiar for some time through the work of Whittington (1959). Remopleuridacea thus afford a second example of secondary conterminant condition having been attained from a natant condition. Unlike at least some of the Asaphacea, the achievement of conterminant hypostomal condition was made by elimination of the preglabellar field by forward encroachment of the glabella – the cephalic doublure remains coincident with the

cephalic rim as it is in ptychoparioids. Even though the conterminant hypostomal condition is functionally the same as it is in asaphaceans it seems possible that the means of achieving it may be different.

Less is known of ventral structures in Dikelocephalacea. Conterminant hypostomal condition certainly pertained in saukiids such as *Saukia*, and also in ptychaspids with a narrow tube-like cephalic doublure, and in dikelocephalids, such as *Dikelocephalus*, with a wide and flat doublure. Idahoiidae may prove to be the sister group of Dikelocephalacea, and idahoïid genera such as *Wilbernia* and *Idahoia* show wide borders, but which do not reach the front of the glabella; these were in all probability still natant.

Proetida. The Order Proetida Fortey and Owens, 1975 includes numerous post-Cambrian families, and was the only trilobite group to survive the Devonian. I shall return to the characters defining it below. Early Proetida, and perhaps the majority of the Order, have natant hypostomal condition. The cephalic doublure closely corresponds with the cephalic rim, the two together forming a tube-like structure in many proetides. Natant hypostomal condition is accordingly obvious for Proetacea having narrow borders and wide preglabellar fields, such as the primitive genus *Decoroproetus* (Owens 1973, pl. 7, fig. 15), and the majority of Aulacopleuridae. On more advanced genera with reduced preglabellar field, such as *Proetus* itself, it is not immediately clear whether the hypostome is or is not attached to the doublure, but specimens preserved 'on their backs' (e.g. *Proetus concinnus* (Dalman), see Owens 1973, pl. 3, fig. 9; Pl. 1, fig. 6 herein) show the hypostome in the fallen position typical of other taxa with natant hypostomal condition. The same lack of attachment of the hypostome probably persisted into the Carboniferous in such genera as *Namuropyge*, which has a preglabellar field, and certain *Cunningella* species (e.g. Woodward 1883, pl. 1, fig. 4a). However, some Proetida *did* attain secondary hypostomal attachment, as shown in text-figure 5. For example, the Carboniferous genus *Paladin* (Whittington 1988b, text-fig. 12) has the glabella encroaching on the cephalic border, and the hypostome is attached to the doublure in the typical conterminant fashion (also text-fig. 5d); the same probably applied to many other Carboniferous phillipsiids. Campbell (1977; also Whittington 1988b) showed that the cephalic doublure on the Devonian brachymetopid genus *Cordania* was relatively wide – wider than the 'border' – and terminated precisely on a line around the front of the preglabellar furrow. If it was in its usual position co-incident with the glabellar frontal lobe it is not unreasonable to assume that the hypostome was conterminant in this case also, although there are no examples known to me of brachymetopids with hypostome *in situ*. Campbell (1977, p. 20) thought that the 'border' furrow in this case was not homologous with that in other Proetida (the contrary opinion was held, for example, by Owens and Thomas 1975), which he regarded as really coincident with the inner doublural margin. If this view is correct then loss of the natant hypostomal condition would be the result of encroachment of the glabella on the border as in *Paladin* and remopleuridids. However, if the other view is held – that the doublure has 'grown beyond' the true border – then the loss of the natant condition was the result of the doublure growing out to meet the hypostomal margin, a case like the Asaphacea described above (and text-fig. 3, top). Whatever the correct interpretation of border homology, these proetaceans evidently show the secondary acquisition of conterminant hypostomal condition by analogous mechanisms to those operating in Asaphina.

Non-proetacean Proetida include several families in Fortey and Owens' (1975) concept. Their original scenario was that these were ultimately derived from the subfamily Hystricurinae, a typically 'ptychoparioid' group with narrow cephalic rims and doublures (e.g. Ross 1951, pl. 8, figs. 7 and 8) and wide enough preglabellar fields to be likely to have had natant hypostomal condition. Early Bathyuridae (*Peltabellia*, see Ross 1951) were generally like hystricurids in these features and there is no reason to suppose that they were other than natant. However, some advanced forms with reduced preglabellar fields, such as *Bathyurus* itself, have been claimed as having rostrum and hypostome in contact (Ludvigsen 1979); Whittington (1988b) also considered that the hypostome was firmly braced in *Bathyurus*. Whittington (1963, pl. 11, fig. 6) figured the cephalic doublure of the bathyurelline *Punka nitida* (Billings) which is wider than in hystricurids but does not extend



TEXT-FIG. 5. Secondly attached hypostomes in Proetida. *a*, *b*, *d*, impendent hypostomal condition in *Griffithides acanthiceps* Woodward; Dinantian, Treak Cliff, Castleton, Derbyshire: *a*, dorsal, and *b*, ventral views, $\times 6$; *c*, oblique ventral view, $\times 5$. Note anterior pits in axial furrows well posterior to usual position in natant forms. National Museum of Wales (NMW) 86.25G.2332. *d*, Secondary conterminant hypostomal condition in *Archegone* (*Phillibole*) aff. *aprathensis* Richter and Richter, Dinantian, slopes of Pendle Hill, Lancashire. $\times 3$, NMW 88.36G.10. Photographs kindly supplied by R. M. Owens.

across the preglabellar field. Ross (1953) described the silicified hypostome of another bathyurelline, *Licnocephala cavigladia* Hintze, which shows remarkably long prong-like anterior wings and a poor match between anterior profile of hypostome and posterior margin of cephalic doublure. It seems then, that in Bathyuridae secondary conterminant condition occurred only rarely, and only in the stratigraphically youngest members of the family. Nor are there any described examples of Dimeropygidae or Glaphuridae in which conterminant hypostomal condition is suspected.

To summarize, Proetida primitively have natant hypostomal condition, and some families remain so. Several other proetide families include advanced members in which the hypostome is secondarily conterminant; this happens by the loss of the preglabellar field by encroachment of the glabella on the border, or, possibly, by widening of the doublure to cover the preglabellar field. The former happens also in the Remopleuridacea; the latter in the anomocarid – asaphid – ceratopygid transition. In no case is there a reversal from conterminant back to natant.

2. *Primary conterminant hypostomal condition.* In the cases just described the conterminant hypostomal condition is derived, within accepted monophyletic groups, from the natant condition. Although these trilobites provide the theme of this paper, it is important to recognize that there are

other trilobite groups with conterminant hypostomal condition in which it is not derived from the natant condition; indeed, it is considered to be the primitive mode of hypostomal attachment for the Trilobita as a whole.

The primitive state: Redlichiida. The Redlichiida are regarded as the sister taxon of all 'higher' trilobites, which excludes only the Agnostida and olenelloids (see text-fig. 14), and includes all ptychoparioids. Redlichiids have functional dorsal ecdysial sutures and have a rostral plate bounded by connective sutures. Following Bergström (1973) and Fortey and Whittington (1989), olenelloids are regarded as primitive trilobites lacking dorsal ecdysial sutures, a view different from that of Lauterbach (1980), who regarded certain olenelloids as more closely related to chelicerates. Ax (1987) summarized Lauterbach's views in English. Here it may be stated that the greater number of derived characters favour the trilobite hypothesis of olenelloid relationships, if the characters identified as synapomorphies by Fortey and Whittington (1989) are correct. The systematic position of the Agnostida is discussed below. If the Redlichiida is correctly identified as the sister group of higher trilobites the redlichiid mode of hypostomal attachment (text-fig. 6) is the primitive one for such trilobites.



TEXT-FIG. 6. Conterminant condition as the primitive hypostomal attachment mode as exemplified in Redlichiida, the sister taxon of 'higher' trilobites. *Redlichia longtangensis* Zhang and Lin (see Zhang *et al.* 1980, text-fig. 53), late Lower Cambrian, Longtang, E. Guizhou, China, showing extension of cephalic doublure and position of hypostome, $\times 1.5$. Nanjing Institute of Geology and Palaeontology 7057. Photograph kindly supplied by W. T. Chang (Zhang Wentang).

Lauterbach (1980) regarded the Emuellidae as the primitive sister group of redlichiids. Pocock (1970, text-fig. 4) clearly described the nature of the attachment of the hypostome in *Emuella*. It is conterminant, the anterior edge corresponding both with the front of the glabella dorsally, and the back end of the relatively narrow (tr.) rostral plate. In *Redlichia* (Öpik 1958; Zhang *et al.* 1980; Whittington 1988a) the hypostomal attachment is similar, that is, conterminant (also *Resserops*, see Hupé 1953, fig. 39). Öpik (1958) showed that the rostral plate and hypostome are fused together in *R. idonea* Whitehouse, whereas in *Emuella* 'the hypostomal suture is functional' (Pocock 1970, p. 528). Of numerous *Redlichia* species figured by Zhang *et al.* (1980) some (e.g. pl. 20, fig. 5) have

hypostomes without attached rostrum, as does *Sardoredlichia* (Rasetti 1972, pl. 9, fig. 19), and it seems likely that the fusion of rostrum and hypostome was an advanced, not a primitive character. Additional evidence for this can be cited in that such secondary fusion happens again, later, in some species only of *Paradoxides* (Whittington 1988a), and in the *Corynexochida*. The important point is that the primitive mode of attachment in the group *Redlichiida* + all other non-olenellid trilobites is conterminant. This can be referred to as *primary conterminant hypostomal condition*. This is **not** homologous with the secondary conterminant hypostomal condition, described above, in which it is derived from the natant hypostomal condition.

Certain redlichiids develop a short preglabellar field: see, for example, *Redlichia yichangensis* Zhang and Lin (*in* Zhang *et al.* 1980) and *R. (Pteroredlichia) chinensis* Walcott (Zhang *et al.* 1980, pl. 25, fig. 5). This does not mean however, that the hypostome became detached from the rostrum and natant. Zhang *et al.*'s pl. 20, fig. 9 and pl. 25, fig. 25 clearly show the hypostome in place beneath the frontal glabellar lobe, and the cephalon in the latter also shows that the posterior part of the rostral plate extends backwards (see text-figure 6) across the 'gap' between marginal rim and preglabellar furrow. Conterminant hypostomal condition is retained. Many redlichiids for which ventral structures are not known show a median plectrum in the preglabellar field (e.g. Zhang *et al.* 1980, pl. 21, fig. 7), and it is my contention that this is the dorsal expression of such a backward extension from the rostral plate. A plectrum is a median backward projection of the border, and usually distinctly defined; however, other redlichiids show a vaguer median depression in the same region, which may still represent the same ventral structure.

Incidentally, whether or not olenellids were trilobites, they do appear to show some comparable ventral structures to redlichiines. Some, such as *Holmia*, were clearly conterminant, with close connection between doublure and hypostome (Whittington 1988a). Others, such as *Olenellus*, show narrow spine-like connections across the preglabellar field, and median plectra dorsally.

Other probable examples of primary conterminant hypostomal condition. If the conterminant hypostomal condition is primitive for the higher trilobites as a whole it is not surprising that it is retained in many families. Some of these were reviewed by Whittington (1988a, b). In some groups the conterminant condition intergrades with the impendent condition discussed in the following section. In many trilobite families the conterminant condition is constant, and retained during modifications to the border. For example, in the calymenid *Neseuretus* (text-fig. 3a) the cephalic border is exceptionally extended for the family and the conterminant hypostomal condition is retained by virtue of an anterior plate-like extension of the hypostomal margin which extends beneath the area between the front of the glabella and the anterior cephalic rim. There is no *a priori* reason why *Neseuretus* should not have become natant – i.e. the hypostome simply 'drifted away' from the rostrum as the border extended – but the fact that this does not happen proves the conservatism of the hypostomal attachment mode.

A list of non-redlichiid higher taxa having primary conterminant hypostomal condition includes the following, most of which I have confirmed through examination of specimens in the British Museum (Natural History) collections. This list is not hierarchically arranged, and those taxa discussed above under secondary conterminant hypostomal attachment are not included.

Order *Corynexochida*: Most of this group are conterminant (text-fig. 3c); a few advanced forms may possibly have been impendent. Loss of hypostomal suture by ankylosis may make the anterior limits of the hypostome difficult to see in some cases.

Superfamily *Leioptegidae*: Apparently all are conterminant, but there are no described examples with hypostome in place. The doublure-hypostome relationship is fairly obvious in those genera, like *Leioptegium* itself (text-fig. 17a, p. 564), with distinct anterior pits far forwards in the axial furrows with which the anterior wings of the hypostome would have engaged. Broad-bordered genera like *Palocorona* Shergold, 1980 develop a 'false border furrow' but the course of the inner margin of the doublure is still revealed by the paradoublural line extending to the front of the glabella.

Superfamily *Damesellacea*: These have not been fully described from the ventral side, but examination of *Stephanocare* and *Blackwelderia* specimens in the B.M. (N.H.) shows that the cephalic doublure is closely

coincident with the cephalic border, which is narrow and ledge-like in front of the glabella, a structure very like that of the Leiostrigeacea. The hypostomes of several genera are known, and assuming the correspondence of anterior wings with the anteriorly placed pits in the axial furrows, it seems likely that the Damesellacea were also conterminant.

Superfamily Cheiruracea: Many entire specimens of cheiruraceans have been described (Lane 1971; Whittington 1988*b*; Jell 1985, pl. 13, fig. 10); all Pliomeridae and Cheiruridae are conterminant, except where the frontal lobe of the glabella has expanded forwards (especially Encrinuridae; some Cheiruridae) and incorporated the border within it, and these may perhaps be better described as impendent.

Superfamily Calymenacea: Advanced calymenids are consistently conterminant, even when, as in *Neseuretus* (above), the preglabellar area is long. The extended preglabellar area in this case is 'covered' by an extension of the hypostome, but this is unusual. Homalonotids with extended (sag.) borders, and such calymenids as *Calymenes* (Derek J. Siveter pers. comm. 1986) cover the extended area by growth of the rostral plate and the adjacent genal doublure. The hypostome remains in its usual position. So far as can be ascertained primitive calymenaceans with preglabellar field were also conterminant. For example *Prionocheilus* (= *Pharostoma*) appears to show a backward extension of the rostral plate sufficient to bridge the distance between anterior border and the front of glabella and hypostome (Whittard 1960, pl. 18, fig. 4).

Suborder Phacopina: Jaanusson (1975) discussed the morphological steps leading to the suborder Phacopina, and described *Gyrometopus* as a primitive representative. This genus had a rather narrow cephalic doublure, but the hypostome is not known and it is difficult to say whether it was or was not conterminant. The more primitive Phacopina are classified within the Dalmanitidae. Many of the stratigraphically early dalmanitids described by Henry (1980) show details of the ventral cephalic surface, including hypostomes in place (Henry 1980, pl. 28, fig. 4; pl. 29, fig. 4). These were probably conterminant. Early Pterygommetopidae, such as *Calypptaulax* (e.g. Chatterton and Ludvigsen 1976, pl. 16) are apparently slightly impendent. Phacopidae are impendent, even early genera such as *Morgatia* (Henry 1980, pl. 43, fig. 6).

Order Odontopleurida: Odontopleurids (text-fig. 3*d*) are known from numerous silicified species; they are all conterminant (see, for example, cephalic shields of several species figured by Chatterton and Perry 1983). Both cephalic border and doublure are narrow, and the hypostome is rigidly attached (Whittington 1988*b*).

Order Lichida: Thomas and Holloway's (1988) recent review of this group shows conterminant condition to be the rule.

This brief review shows that, although the conterminant condition is primitive for the higher Trilobita, it is present, and consistently so, within a variety of higher taxa extending to the later history of the group. While it is likely that in mid-Cambrian groups this is a retained plesiomorphic character, there is at least the possibility among later groups such as the Calymenacea that it is secondarily derived from the natant condition, as in Asaphina and Proetida, and if so this would have considerable taxonomic implications. I return to this topic below.

Impendent hypostomal condition

In the impendent hypostomal condition (text-figs. 1*c*, 5*a-c*) the close relationship between the position of the hypostome and the front of the glabella which pertains in natant or conterminant hypostomal condition is lost. The term was coined by Fortey and Chatterton (1988) with reference to Cyclopygacea, but applies to many other groups. Its taxonomic importance is proved by the fact that there is no known example where impendent hypostomal condition reverts to conterminant or natant. The impendent condition results from the relative forward growth and often inflation of the glabella to engulf the cranial border; in the process the anterior glabellar margin more nearly coincides with the cephalic margin, and the hypostomal suture occupies a relatively posterior position. The relationship between the anterior wing of the hypostome and its connection in the axial furrow is not lost. This is shown by the hypostomes of *Nileus* and *Remopleurides*, for example, in which the anterior hypostomal wings become elongated in the dorsal direction (e.g. Whittington 1965, pl. 31, figs. 2 and 3; 1988*b*, text-figs. 5 and 6). Impendent hypostomal condition can characterize higher level taxa (Cyclopygacea, Illaenina, Phacopidae), and is independent of the development of the ventral sutures, occurring with rostral plate (*Illaeus*), median suture (*Amphytrion*) or fused cheeks (*Symphysurus*, *Phacops*).

In those groups which attained secondary conterminant hypostomal attachment a number of subgroups went further to become impendent (Cyclopygacea, some Asaphinae, some phillipsiids

such as *Griffithides* and *Hentigia*, see Whittington 1988b). It is clear in these that there is a morphological and phylogenetic progression running natant – secondary conterminant – impendent. Impendent hypostomal condition may have been capable of developing directly from primary conterminant condition. But in, for example, *Corynexochida* (*Corynexochus*) having the glabella extending far forwards it is likely that the rostral plate became extremely narrow (sag.) and impendent attachment was not attained.

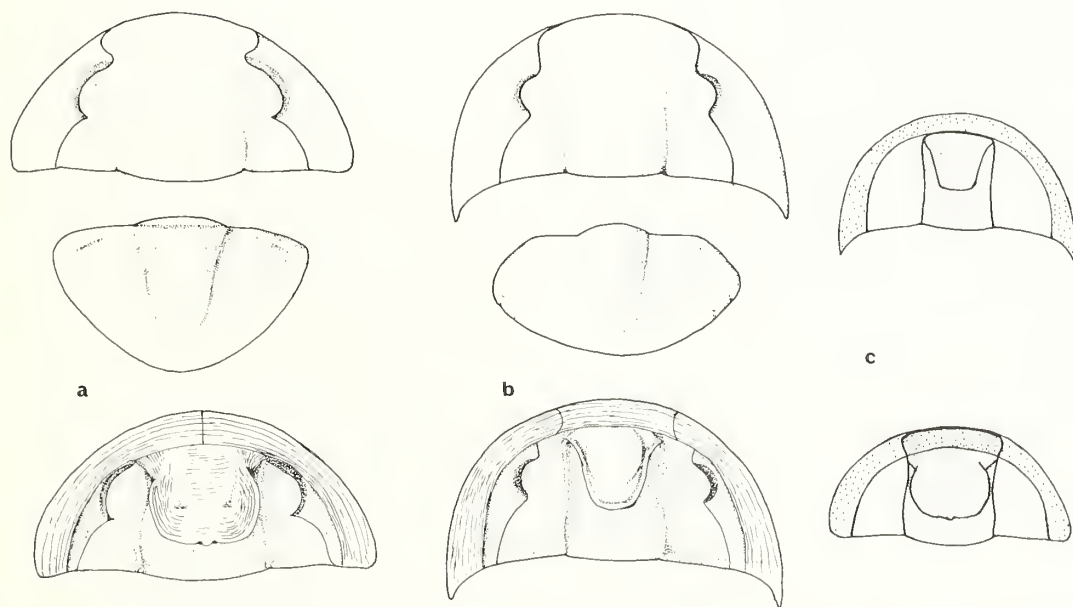
A detailed discussion of the impendent condition is not as important to the phylogenetics of Ptychopariida as is the conterminant condition, but it is important in the wider context of trilobite classification. In addition to those Asaphina mentioned already several large groups are typified by having impendent hypostomal condition:

Superfamily Illaenacea: as restricted to Illaenidae plus Scutelluidae, and excluding groups placed in Proetida by Fortey and Owens (1975). Even early members of this group such as *Raymondaspis* (Whittington 1965, pl. 57, fig. 9) appear to have the glabella extending well beyond the inner doublural margin.

Advanced Phacopida: The Phacopidae, Calmoniidae and Monorakidae are all impendent. The first two of these groups had their origins in the Ordovician, and presumably had sister groups within what would at present be classified as dalmanitaceans having conterminant hypostomal condition.

Late Proetida: A number of stratigraphically late genera of Proetida have glabellas that expand forwards to the cephalic margin – much in the manner of Nilcidae in the Asaphina. Examples would include the Permian genus *Paraphillipsia* (see Owens 1983), and *Griffithides* (text-fig. 5a–c). Because such forms had cephalic doublures of normal width they would have had impendent hypostomal condition also. They must have been derived from one of the secondarily conterminant proetides.

One example will suffice to show that the discrimination of the different modes of hypostomal attachment can be of immediate taxonomic use (text-fig. 7). Bornemann (1883) described the trilobite *Illaenus meneghinii* from Sardinia, which subsequently became the type species of



TEXT-FIG. 7. Hypostomal attachment condition as a key to revealing homoeomorphy. *a* and *b*, dorsal cephalic and pygidial morphology of the early Ordovician genus *Platypeltoides*, and the early Cambrian genus *Giordanella* (after Rasetti 1972) showing general similarity, *c*. $\times 3$. Below, inferred ventral views of the same. *c*, cartoons illustrating hypostomal attachment mode using same conventions as in text-figure 1, *Giordanella* above, probably conterminant, *Platypeltoides* below, impendent.

Giordanella. Because of the general resemblance of *Giordanella* to early Ordovician Nileidae, the beds yielding it came to be regarded as transitional between Cambrian and Ordovician. Later it became apparent that the horizon was, in fact, Lower Cambrian, and the time gap between this horizon and the early Ordovician was so considerable that Nicosia and Rasetti (1971) rejected nileid affinities in favour of *incertae familiae*. Rasetti (1972, p. 44) went further in using *Giordanella* as a good example of how homoeomorphy confuses and, by implication, as part of his argument on how misleading the morphology of Cambrian trilobites can be 'without taking into consideration the age and geographic province'. In the present context, it is clear that, effaced dorsally though it is, the cranidium of *Giordanella* can show the anterior outline of the glabella (e.g. Rasetti 1972, pl. 10, figs. 3, 9) well inside the cranial margin. The Family Nileidae, and the superfamily Cyclopygacea to which it belongs, are characterized as having impendent hypostomal condition, and as a consequence the glabella dorsally extends to the cephalic margin. There is thus an easy way to show that *Giordanella* and, for example, the nileid *Platypeltoides*, a genus it generally resembles dorsally (text-fig. 7), are not related. If one adds to this the fact that *Giordanella* has a wide rostral plate (Rasetti 1972, pl. 10, fig. 22) whereas the Nileidae either have a median suture or fused cheeks, then the likelihood of a close taxonomic relationship between nileids and *Giordanella* becomes remote. *Giordanella* probably had primary conterminant hypostomal condition, if we are to judge from the width of the doublure and the indication of a paradoublural line running to the front of the glabella. This suggests a comparison with the family Ellipsocephalidae, which is widespread and familiar in the Lower Cambrian. *Giordanella* would then become just another example of a relatively macropygous and effaced trilobite, which is known to be one of the most iterative (and therefore of least taxonomic moment) trends in trilobite evolution (Lane and Thomas 1983). One might perhaps turn Rasetti's argument on its head and use this example to demonstrate that it is necessary to look at characters critically first before jumping to stratigraphical conclusions based on general resemblance.

NATANT HYPOSTOMAL CONDITION AS A SHARED DERIVED CHARACTER

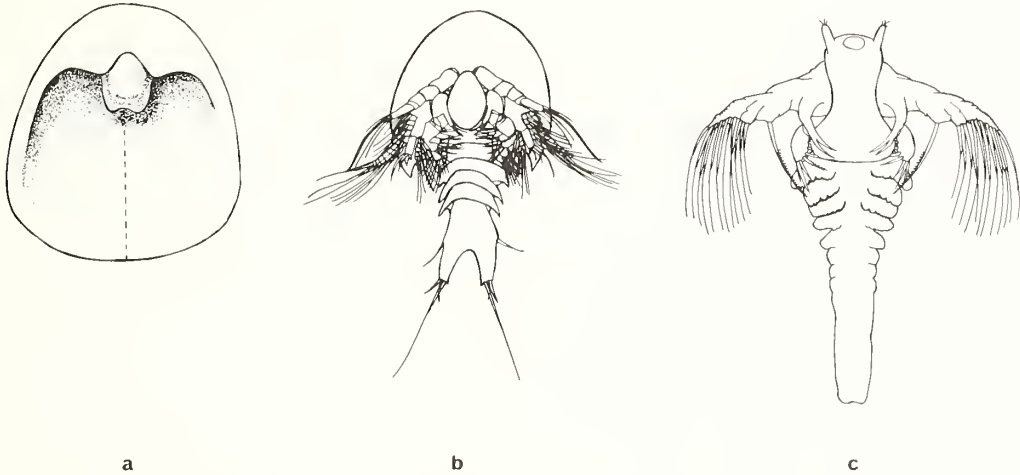
It was concluded above that the primitive hypostomal attachment mode is conterminant. If so, the natant condition is a derived character and hence a synapomorphy of potential use in defining a monophyletic group. Öpik (1963, p. 77) has already stated that the natant hypostomal condition is of importance in higher level trilobite classification. There are a few criteria which can be used to establish the polarity of a character shift (Schoch 1986, pp. 134–142) – in this case, that the natant condition is a derived character. The comparison with *Redlichia* described above exemplifies the criterion of comparison with the out-group. There is also the criterion of ontogeny: during morphogenesis the developmental sequence should parallel the inferred polarity (conterminant to natant in this case). The stratigraphic criterion suggests that the primitive condition will also be stratigraphically earlier. Whittington (1988a) has shown that the natant condition (his 'detached') pertained in the type species of *Ptychoparia* – and so it will be, by definition, a ptychoparioid character. In order to establish how unusual the natant hypostome is as a derived character it is also worth looking at a wider range of arthropod out groups. If unusual, then it is reasonable to attribute to it some 'weight' in classification.

How unusual a character is the natant hypostome?

The relationship of the trilobites to the other Arthropoda is not resolved (Cisne 1974; Hessler and Newman 1975; Lauterbach 1980; Schram 1986). Most authors would agree that they are part of a clade that includes both crustaceans and arachnates. A preliminary cladistic analysis by Briggs and Fortey (1989) indicated that the trilobites were advanced relative to crustacean groups. Antennae and biramous trunk limbs were primitive attributes of the crustacean/arachnate clade. There is no occasion here to discuss the different theories of trilobite relationships but it is worth considering the Crustacea as an out-group for hypostomal attachment. The homologue of the hypostome may be the labrum (labral plate if sclerotized), and, if so, 'labral plate' is probably the

correct morphological term for hypostome, although it has been used by few authors (e.g. Jaanusson 1975). In crustaceans the labrum *is* attached to and continuous with the dorsal cuticle. There is no consensus about what constitutes the most primitive living crustacean, but the attached labrum applies whether this is taken as a remipede (Schram 1986), or a cephalocarid (Sanders 1963) or a notostracan (text-fig. 8). The same attachment is observed even in highly specialized crustacean groups such as the copepods (Boxshall 1982, text-fig. 46), and is apparently invariable. In the nauplius larva, which is generally regarded as primitively present in Crustacea, the labrum is prominent (text-fig. 8), and a comparison may be drawn with the prominent hypostome of trilobite protaspides.

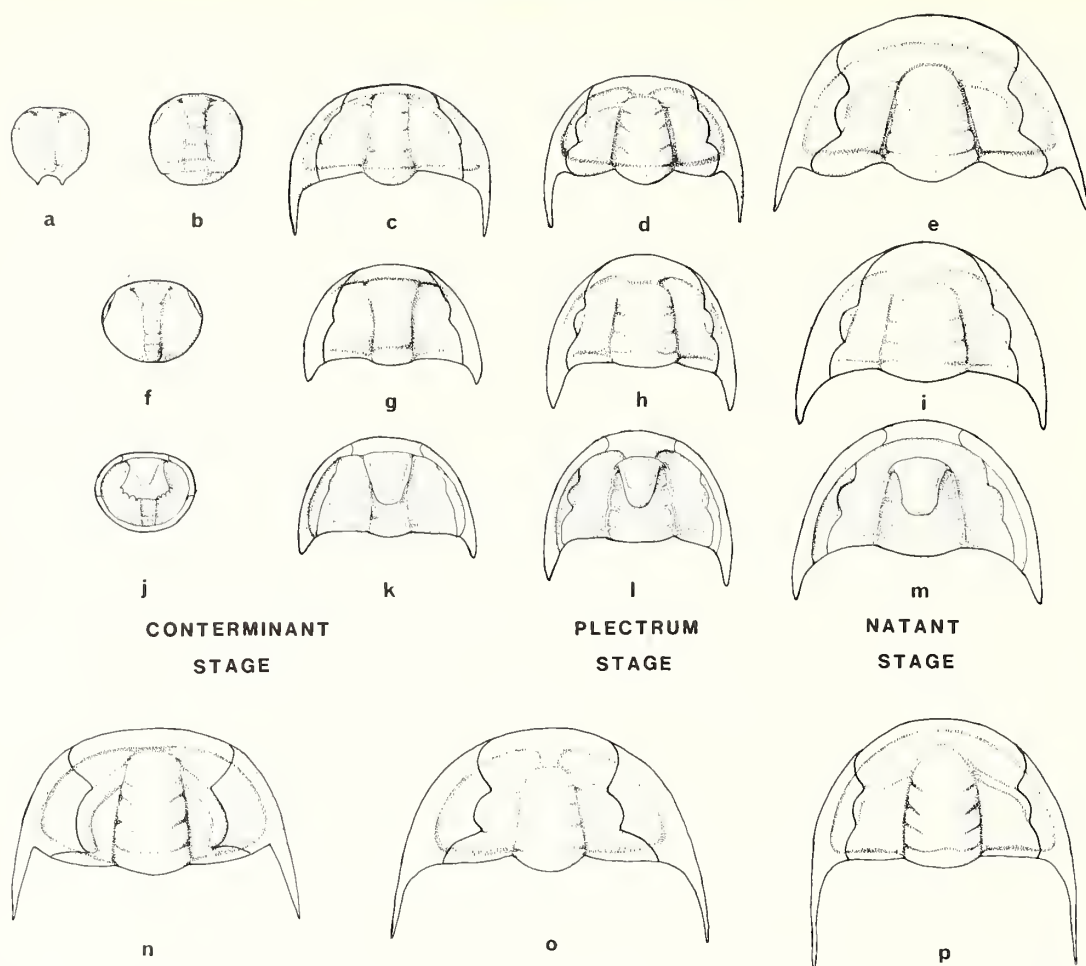
Hence, if the attached labral plate is so widespread among these crustacean groups, then the detached, natant condition becomes the more unusual as an advanced, apomorphic character.



TEXT-FIG. 8. Labral plate attached to carapace in primitive crustaceans and their early growth stages. *a*, carapace of notostracan *Triops*; *b*, immature cephalocarid *Hutchinsoniella* (after Sanders 1963); *c*, anostracan *Artemia* nauplius (after Sanders 1963).

Ontogenetic evidence for character polarity

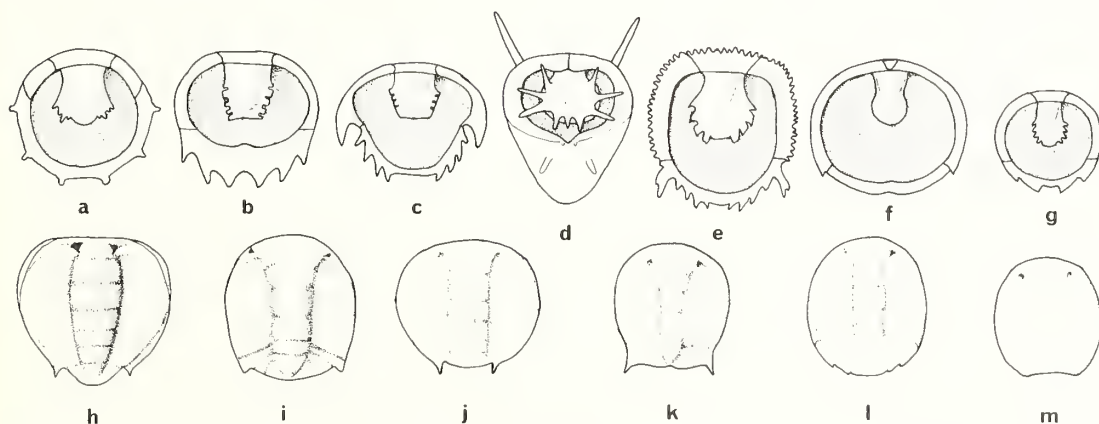
Trilobites are unusual among fossil groups in having the exoskeletal ontogeny nearly completely preserved, and described from numerous taxa. It is feasible to see how the natant hypostomal condition arises during ontogeny. The earliest larval stage is the protaspis. Protaspides of some species are known with the hypostome in place, but many more are known from the dorsal shield minus cheeks. The hypostome is invariably prominent in complete protaspides, occupying a relatively large area of the venter by comparison with meraspides or adults. In all protaspides from which the hypostome is described it was attached to the doublure (see, for example, Whittington *in* Moore 1959; Fortey and Chatterton 1988, fig. 10; text-fig. 10*a-g* herein). The protaspis did not have natant hypostomal condition. Even in those protaspides for which the hypostome is not known it can be inferred that it was attached. This is because the anterior pits are often prominent near the anterior margin of the glabella, and the glabella extends far forwards (see text-fig. 10*h-m*), so that the correspondence of anterior pits with hypostomal attachment means that the hypostome had to be adjacent to the cephalic doublure in the usual position. The prominence of the anterior pits in many protaspides is presumably a reflection of the large relative size of the hypostome. Such prominent pits are even visible on smoothed out, planktic, asaphoid protaspides such as those of asaphids (Tripp and Evitt 1986), nileids (Fortey and Chatterton 1988) and remopleuridids (Whittington 1959), where they may afford the only evidence of the extent of the cephalic axis (text-fig. 10*m*). The only possible exceptions are discussed below.



TEXT-FIG. 9. Natant hypostomal condition as a derived character. Ontogenies of typical ptychoparioids, showing change from conterminant to natant, by way of a plectrate stage. *a-e*, *Elhmanella waptaensis* Rasetti (after Hu 1986, text-fig. 11), Middle Cambrian, Canada, dorsal views; *a*, small protaspis, $\times 20$; *b*, large protaspis, $\times 16$; *c*, meraspis cranidium *c.* $\times 15$; *d*, late meraspis, $\times 5$; *e*, holaspis, $\times 5$. *f-m*, ontogeny of *Crassifimbria* (after Palmer 1958), Late Lower Cambrian, Nevada, dorsal (*f-i*) and ventral (*j-m*) views of comparable stages. The rostral form at the 'plectrum stage' is not yet described for this species, but is inferred from such specimens as that depicted by Zhang and Jell (1987, pl. 80, fig. 1 *n-p*); the ontogenetic series is matched by adult cranidial morphologies among Lower Cambrian trilobites, which may record the evolutionary steps involved in the origin of natant groups; *n*, *Redlichia* (after Zhang *et al.* 1980); *o*, *Dolerolenus* (after Rasetti, 1972); *p*, *Hamatolenus*.

Hence during ontogeny the hypostome of trilobites with adults having the natant hypostomal condition must have become separated from the doublure. How this may have happened in Ptychopariidae has already been well described in *Crassifimbria* (Palmer 1958) and can be inferred from the ontogeny of other 'generalized' ptychoparioids such as *Elhmanella* (Hu 1984, 1986). Protaspides of such ptychoparioids are all very similar (Palmer 1962; Hu 1971; text-figs. 9, 10*h-m* herein) having a narrow axis with transverse annulations of varying inflation, the anterior of the axis expanding in width near the front margin of the protaspis. During the meraspis stage (text-fig. 9), a distinct frontal cranidial border appeared (e.g. Palmer 1958, pl. 26, fig. 4), with which the doublure

corresponds ventrally, but at this stage the glabella still reached the border, and it is a reasonable interpretation that the hypostome was attached and conterminant. Subsequent growth allows for the appearance of the preglabellar field, at first narrow, and widening during subsequent instars. This marks the separation of border from glabella, and presumably the detachment of hypostome from doublure, with the onset of the natant hypostomal condition. In both *Crassifimbra* and *Elmaniella* this happens during the later meraspis. The conterminant stage is separated from the natant by a phase in which the border furrow curves towards the glabella as a plectrum (plectrum stage in text-fig. 9). In the ontogeny of *Sao* (Whittington *in* Moore 1959) the degree 1 meraspis was conterminant, the degree 6 meraspis natant. Thus the ontogeny (conterminant to natant) parallels the inferred phylogeny. Again this is consistent with the recognition of the natant condition as a synapomorphy. Adult trilobites representing the plectrum stage are described from several families (e.g. text-fig. 9). In those Ordovician forms known to be *secondarily* conterminant from phylogenetic analysis, there is no evidence to suggest that they went through a natant growth stage during ontogeny (e.g. Asaphidae; Tripp and Evitt 1986) and so the mature conterminant condition was attained by its retention and displacement into the adult, essentially a process of paedomorphosis. However in certain Cambrian genera there is evidence to suggest that there may still be an intervening natant phase of ontogenetic development (i.e. the sequence may run attached hypostome – free – secondarily attached). In *Auritama trilunata*, illustrated by Öpik (1967, pl. 15, figs. 3–6), a series of cranidia ranging through probable meraspis to large holaspis show a progressively widening border and reduced preglabellar field, the border being known to correspond with the cephalic doublure. It is not known whether the hypostomal attachment became secondarily conterminant in this species, although the close coincidence of border furrow and preglabellar furrow in the largest cranidium suggest that it may well have been so.



TEXT-FIG. 10. *a-g*, attachment of hypostome to doublure as the general condition in larval trilobites, illustrated by protaspides of major trilobite groups shown from the ventral side. *a*, Ptychopariina, *Aphelaspis* (after Palmer 1962); *b*, Lichida, *Acanthopyge* (after Chatterton 1971); *c*, Scutelluina, *Dentaloscutellum* (after Chatterton 1971); *d*, Asaphida, *Isotelus* (after Evitt, 1961); *e*, Phacopida (Calymenina), *Flexicalymene* (after Fortey and Chatterton 1988); *f*, Proetida, *Proetus* (after Chatterton 1971); *g*, generalized Ptychopariina, *Spencella* (after Fortey and Chatterton 1988). Not to scale. *h-m*, dorsal views of Cambrian libriformate protaspides of various families showing general (plesiomorphic) similarity, and frontal position of anterior pits indicating that the hypostome was attached to the doublure on the ventral surface. These protaspides are arranged in order of greater effacement from left to right. *h*, late protaspis of *Leptoplastus* (Olenidae) (after Whitworth 1970), $\times 60$; *i*, late protaspis of *Welleraspis* (Catillicephalidae) (after Rasetti 1954), $\times 50$; *j*, late protaspis of *Dytremacephalus* (Pterocephaliidae) (after Hu 1971, pl. 16, fig. 4), $\times 50$; *k*, late protaspis of *Hardyoides* (Menomoniidae) (after Palmer 1962), $\times 60$; *l*, late protaspis of *Dunderbergia* (Alokistocaridae) (after Hu 1971, pl. 15, fig. 8), $\times 50$; *m*, early protaspis of *Glyphasps* (Anomocaridae) (after Hu 1971, pl. 11, figs. 1 and 2), $\times 50$.

Relatively little is known about early Cambrian redlichiid ontogeny. Kobayashi and Kato (1951) described the ontogeny of *Relichia chinensis* Walcott, and figured an early conterminant stage. This has been augmented by Zhang *et al.* (1980) who have described ontogenetic series of *Redlichia takooensis* Lu and *R. (Pteroredlichia) murakamii* Resser and Endo, including a protaspis stage. By early meraspis stage (Zhang *et al.* 1980, pl. 23, figs. 5–7) there was a distinct, ledge-like anterior border, and it is likely that the hypostome was conterminant. As in olenellids *Redlichia* larvae show well-developed palpebro-ocular ridges which curve strongly backwards. Palmer (1957) described the ontogeny of *Olenellus*, which apparently lacked a protaspis stage; by the early meraspis hypostome and doublure were connected only by a median prong, which appears to be the same condition as pertained in adult olenellids having a preglabellar field. Palmer and Halley (1979) described the ontogeny of another olenellid, *Bristolia*, in which it seems likely that the conterminant condition pertained throughout ontogeny, because the border and preglabellar furrow remain in contact. Because the redlichiids rather than the olenellids are likely to be the primitive sister group of the ptychoparioids the ontogeny of olenellids is less relevant to trilobites having natant hypostomal condition. The familiar mid-Cambrian redlichiine *Paradoxides* is presumably conterminant throughout ontogeny. The ontogenies of early representatives of trilobites with natant hypostomal condition will prove relevant to the morphogenesis of the structures involved, but little is known at present. A critical group may prove to be the Protolenidae. *Protolenus* itself was probably natant in the adult, with the glabella falling well short of the border; closely related genera such as *Myopsolenus* certainly were natant, as shown by specimens showing the inner margin of the cephalic doublure (e.g. Bassett *et al.* 1976, pl. 1, fig. 1) which is well-removed from the preglabellar furrow. Romanenko (1977, pl. 13, figs. 3–5) described *Protolenoides fasciferrus*, and included a figure of a meraspide cranidium which appears to be of the usual ptychoparioid type, and hence presumably had an attached hypostome. Small, submature cranidia of the same species show a strong plectrum extending to the glabellar front. If this represents the dorsal expression of a backward extension of the rostrum then it might be suggested that the hypostome was still in primary conterminant attachment mode. The plectrum is less distinct in fragmentary larger cranidia. Plectra are also present in some other protolenids (*Bergeroniaspis*, *Olekmaspis*), and in Dolerolenidae (*Dolerolenus* – see Rasetti 1972, pl. 15, fig. 4). I would speculate that this plectrate condition might represent the transition between primary conterminant and natant hypostomal condition as shown in text-figure 9. Interestingly, it parallels the situation in *Proceratopyge* (e.g. Rushton 1983, text-fig. 6b; Jago 1987; text-fig. 3b herein) in which the reverse was happening: as the hypostome achieved secondary conterminant hypostomal condition a plectrum is developed dorsally corresponding with a backward extension of the cephalic doublure (in this case including a median suture). The ontogeny of the Corynexochida, in which the hypostome remained attached to the doublure throughout growth, was described by Robison (1967).

Stratigraphic evidence for natant condition as a derived character

International correlation of early Cambrian rocks is still controversial. However, in no section with a relatively complete sequence does a ptychoparioid appear first below a redlichiid (Brasier 1989). Hence so far as it goes the stratigraphic record is in accord with the proposed character polarity.

To summarize, ontogeny and stratigraphy confirms the conclusion drawn from comparison with other arthropods, and from the phylogenetic analysis of trilobite relationships used by previous authors, that an attached hypostome is primitive and the natant hypostomal condition a derived character. It is concluded that *those trilobites having natant hypostomal condition can be regarded as constituting a monophyletic group*. Those trilobites which were *primitively* natant, but secondarily conterminant, such as were discussed above, belong within the same group.

Distribution of natant hypostomal condition in the various trilobite families

There now follows an inventory of trilobite families in which the natant hypostomal condition occurs, or can be reasonably inferred to occur, with documentation. Some examples are illustrated

on Plate 1; for most others a literature reference is given, either showing the hypostome as it fell into the forward part of the glabella upon decay of the soft parts, separated from the cephalic doublure, or showing that the extent of the cephalic doublure fell short of the preglabellar furrow. Some modes of hypostomal attachment were described in detail by Whittington (1988*a, b*). The list is not exhaustive, in that one or two examples are sufficient for each family, and there may be additional families for which I have not found evidence. For convenience families are arranged alphabetically. Families are accepted uncritically, although many are not satisfactory, monophyletic taxa. Even so I cannot accept Raymondinidae, which is an absurdly heterogeneous collection of genera in the *Treatise*.

Agraulidae. *Agraulos* was discussed in detail by Whittington 1988*a*.

Alokistocaridae. See *Elrathia* (Pl. 1, fig. 6).

Anomocaridae. See discussion in Fortey and Chatterton (1988); *Anomocarioides limbatus* (Egorova *et al.* 1982, pl. 44, fig. 2).

Andrarinidae. A somewhat doubtful taxon. Dean (1972) illustrated narrow cephalic doublure of *Holasaphus*, which shows likelihood of natant hypostomal condition. Although *Holasaphus* was placed in this family by Howell (*in* Moore 1959), it was assigned with question to Ptychopariidae by Dean.

Asaphiscidae. *Blainia*, see Pl. 1, figs. 2, 8.

Aulacopleuridae. Natant condition can be inferred on *Aulacopleura* with narrow and tubular cephalic doublure and wide preglabellar field.

Auritamiidae. See ontogenetic series of *Auritama trilunata* (Öpik 1967, pl. 15, figs. 3–6.) and discussion above (p. 547).

Bathyruridae. See discussion above (p. 538); most bathyurids are regarded as likely to have been natant except *Bathyrurus* (Whittington, 1988*b*).

Cedariidae. *Cedaria* (Pl. 1, fig. 3).

Conocoryphidae. Probably a polyphyletic family, united only by secondary blindness. *Conocoryphe* itself discussed in detail by Whittington (1988*a*).

Dimeropygidae. This family is problematic, in that *Dimeropyge* has a curious rostral plate (Tripp and Evitt 1983, pl. 33, fig. 11; Chatterton and Ludvigsen 1976, fig. 8) with a prong-like extension which may have engaged with the unusually small hypostome (which has reduced anterior wings). If this is so it qualifies as a unique form of (derived) hypostome attachment, and is neither natant nor conventionally secondarily conterminant. On the other hand I have searched inside entire cephalic shields of early dimeropygids such as *Ischyrotoma anataphra* Fortey, 1979 without finding any sign of an attached hypostome, and I think it likely that these early forms were natant.

Dokimocephalidae. Little known of ventral surface. Narrow doublure of free cheeks shown in *Wulmia* by Zhang and Jell (1987, pl. 119, fig. 5) and natant condition likely in this member of the family.

Ellipsocephalidae. Šnajdr (1958) has illustrated the cephalic doublure of the type species of *Ellipsocephalus*, which demonstrates the likelihood of a gap between hypostome and doublure.

Hapalopleuridae. *Skjarella* sp., a new discovery in the Tremadoc of Shropshire by myself and R. M. Owens (in prep.) shows natant condition in entire specimen with hypostome in place.

Idahoïidae. *Saratogia*, narrow width of genal doublure illustrated by Ludvigsen and Westrop (1983, pl. 8, fig. 10); if this followed border furrow on cranidium then natant condition pertained.

Loganopeltidae and Harpididae. Lower lamella in *Harpides* falls well short of glabellar front (holotype of *H. grimmii* Barrande, 1872 shows hypostome in place). These two families are united by some authors.

Lonchocephalidae. Rasetti (1954, pl. 62, fig. 13) illustrated narrow genal doublure, and rostral suture of *Wellerspiss swartzi*. It is possible that some lonchocephalids lacking preglabellar field were secondarily conterminant (*cf.* Whittington 1988*a*).

Marjumiidae. See Robison (1964, pl. 10, figs. 10–15) for silicified specimens of *Modocia* showing how doublure falls short of preglabellar furrow.

Menomoniidae. *Bolaspidella* discussed by Whittington 1988*a*.

Nepeidae. *Penarosa netenta*, see Jell (1977, especially pl. 21, figs. 5, 7).

Olenidae. Diagnosis in Nikolaisen and Henningsmoen 1985; *Peltura* see Henningsmoen (1957, pl. 26, fig. 2); *Porterfieldia* (Fortey and Owens 1978, pl. 1, fig. 5); *Parabolinella* (Whittington 1988*a*); *Hypernecaspis* (Pl. 1, fig. 1). Some of the *in situ* hypostomes seem to be too small to have been attached by the anterior hypostomal wings as suggested by Whittington 1988*a*. Some derived forms which have lost the preglabellar field (*Triarthrus* see Whittington and Almond 1987) may have become secondarily conterminant.

Papyriaspidae. Doublure of free cheek of *Papyriaspis lanceola* figured by Öpik (1961, pl. 17, fig. 3).

Parabolinoiidae. See, for example, Westrop (1986, pl. 18, fig. 18) for narrow genal doublure coinciding with border in *Orygmaspis* (*Parabolinoidea*) species with wide preglabellar field.

Proetidae. *Proetus* (Pl. 1, fig. 7) and *Decoroproetus*, see Owens (1973) for specimens preserved from ventral side with hypostomes nearly *in situ*.

Protoleniidae. *Hamatolenus* see Bassett *et al.* 1976, and comments above.

Pterocephaliidae. *Strigitambus? blepharina* (Palmer 1968, pl. 16, fig. 15), *Litocephalus* (Palmer 1960, pl. 8, figs. 13, 16). See also discussion in Fortey and Chatterton 1988, which excludes *Aphelaspis* (also natant) from this family.

Ptychopariidae. *Ptychoparia striata* (see Whittington 1988a); *Asthenopsis* (see Jell 1978a). Šnajdr (1958, pl. 40, fig. 3) showed *Ptychoparia* hypostome in near-life position.

Remopleuridacea. *Richardsonella* (see Palmer 1968, pl. 14, fig. 8); *Elkanaspis* (see Ludvigsen 1982 for silicified specimens showing narrow cephalic doublure combined with wide preglabellar field).

Solenopleuridae. *Sao*, discussed in Whittington 1988a.

Trinucleidae. Statement in Hughes *et al.* (1975, p. 541); Whittington (1988b, p. 328).

This long list proves two important points:

1. If the natant hypostomal condition defines a monophyletic group as argued above, it is retained in a variety of families within that group – it is generally a stable character.

2. Within this group it is also a primitive character, being shared with the common ancestor of the group. This means that it is of *no consequence in defining phylogenetically based subgroups*. This is the usual situation where a synapomorphy becomes symplesiomorphic at the next level in the taxonomic hierarchy (Eldredge and Cracraft 1982). Hence within the group defined by having natant hypostomal condition, any subgroups have to be defined on other, derived characters.

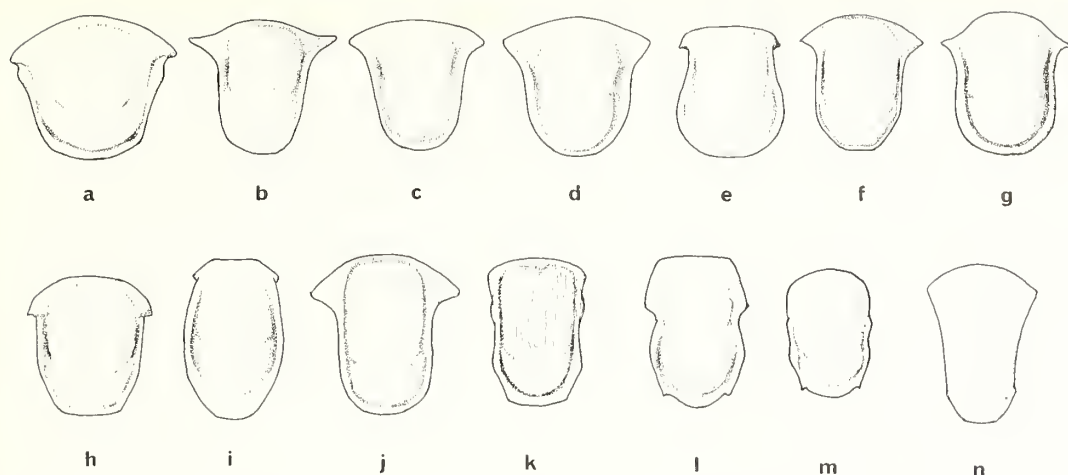
This means that natant hypostomal condition is of use in suggesting common ancestry, but we must look to other characters to define natural groups within this great assemblage of trilobites. Those groups (currently Asaphina, Proetida) with secondarily conterminant or impendent hypostomal condition belong within the overall natant group, and have to be defined on other derived characters – for example, the Asaphina are defined by having a median suture – and the fact that early members of the group have natant hypostomal condition while later ones generally have attached hypostomes (Fortey and Chatterton 1988) supports their common ancestry, but does not greatly help with the definition of the group. A definition of Proetida is given below.

If the natant hypostomal condition is correctly regarded as a synapomorphy then the natural group having it, or only secondarily losing it, needs a name. For this group I propose the name **Libristoma**. The taxonomic status of the Libristoma is discussed in more detail below; it is a more inclusive group even than the Order Ptychopariida.

HYPOSTOME ATTACHMENT AND HYPOSTOME SPECIALIZATION

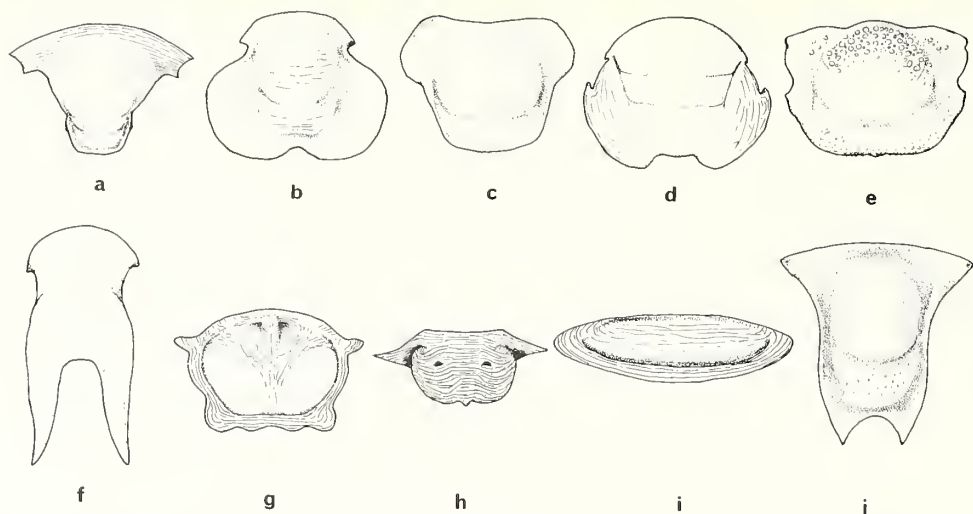
One of the consequences of the natant hypostomal condition seems to have been that, upon the death of the trilobite, or during moulting, the hypostome was easily separated from the rest of the exoskeleton. I do not think it is a coincidence that most of the families listed above have very few species for which the hypostome is definitely assigned. Of dozens of species of Ordovician trinucleids only two to my knowledge have hypostomes associated, and the figure is similar for many Cambrian families, and some (e.g. Dokimocephalidae) apparently have no hypostome yet associated. Conversely, unassigned hypostomes, all very similar, are often figured at the end of monographs on Cambrian trilobites (e.g. Palmer 1960, pl. 11). Cambrian families with conterminant hypostomal condition, such as Redlichiidae, Paradoxidae or Corynepochidae, have numerous species with definite assignment of hypostomes. The same applies to those families (Asaphidae, Nileidae) in which secondary hypostomal attachment has occurred. Nonetheless in natant families when the right kind of ventral-side-up preservation occurs the hypostomes are found in the appropriate position, and I see no grounds to suppose that there were species which lacked hypostomes altogether.

On gathering together information on the hypostomes which *have* been assigned to trilobites



TEXT-FIG. 11. The conservative morphology of hypostomes from trilobites having natant hypostomal condition, illustrated by hypostomes of species belonging to several families and ranging in age from Lower Cambrian to Carboniferous (top left to bottom right). *a*, yinitid redlichiid *Drepanopyge* (after Zhang *et al.* 1980, pl. 51, fig. 9), showing how this primitive morphology is retained in natant trilobites, $\times 2$. Natant hypostomes: *b*, *Crassifimbria* (Ptychopariidae), Lower Cambrian (after Palmer 1958, pl. 25, fig. 13), $\times 10$; *c*, *Conocoryphe* (Conocoryphidae), Middle Cambrian (after Šnajdr 1958, pl. 34, fig. 4), $\times 4$; *d*, *Ptychoparia striata* (Ptychopariidae), Middle Cambrian, (after Šnajdr 1958, pl. 40, figs. 3, 5), $\times 2.5$; *e*, *Dunderbergia* (Alokistocaridae), Upper Cambrian (after Hu 1971, pl. 15, fig. 30), $\times 10$; *f*, *Aphelaspis* (regarded as Pterocephaliidae), Upper Cambrian (after Rasetti 1965, pl. 20, fig. 9), $\times 5$; *g*, a hystricurid, early Ordovician (after Ross 1951, pl. 19, fig. 3), $\times 9$; *h*, *Parabolinella* (Olenidae), early Ordovician, $\times 4$; *i*, *Bathyrurellus* (Bathyruridae), early Ordovician (after Fortey 1979, pl. 31, fig. 9), $\times 3$; *j*, *Paraproetus*, (Proetidae), late Ordovician (after Owens 1973, pl. 12, figs. 12*a* and *b*), $\times 7$; *k*, *Proetus* (Proetidae), Silurian (after Owens 1973, pl. 4, fig. 19), $\times 4$; *l*, *Koneprusites* (Proetidae), Devonian (after Šnajdr 1980, pl. 51, fig. 10), $\times 6$; *m*, *Voigtaspis* (Proetidae), Devonian (after Šnajdr 1980, pl. 52, fig. 11), $\times 3$; *n*, *Phillipsia* (Phillipsiidae), Carboniferous (after Woodward 1883, pl. 2, fig. 6), $\times 3$.

having natant hypostomal condition another fact becomes clear. The hypostomes of trilobites with natant hypostomal condition tend to be as similar as they are unremarkable (Whittington 1988*a*, p. 604; text-fig. 11 herein). What they share is an elongate (sag.) oval middle body, carrying a pair of usually rather short middle furrows often posterolaterally placed; rather narrow (tr) lateral borders, and a rounded to transverse posterior border without a fork, or other marginal modification; a pair of small posterolateral spines may or may not be present. Hypostomes of this kind can be found from the Lower Cambrian to the Upper Palaeozoic. The hypostomes of some redlichiid and dolerolenid trilobites are virtually identical (e.g. *Dolerolenus*, see Rasetti 1972, pl. 16) and the obvious inference is that this 'ptychoparioid' hypostome is a retained primitive character. As the redlichiid ancestor of the Libristoma acquired the natant hypostomal condition, the hypostome became, as it were, morphologically frozen. Surface sculpture on many of these hypostomes was lacking, or at most finely granulate, and only became at all complex on some proetids. The cephalic doublures of most 'ptychoparioids' carry terrace ridges. We can contrast the conservatism of the natant hypostome with the new features in morphology that arise in secondarily conterminant and impendent hypostomes (text-fig. 12). Posterolateral hypostomal borders can become very wide (Nileidae); posterior forks can develop (most Asaphidae, *Hypodicranotus* in the Remopleuridae); the overall shape can become greatly elongate (Brachymetopidae) or transverse (Cyclopygidae); maculae may become prominent (*Remopleurides*) or absent (the cyclopygid *Degameilla*). The terrace ridges hitherto largely confined to the cephalic doublure appear to 'spread onto' the hypostome and may be as prominent, or even more prominent, as they are upon the



TEXT-FIG. 12. Hypostomes of trilobites in which the hypostome was attached to the doublure in either impendent or conterminant mode, showing various kinds of specialization, in contrast to the natant hypostomes shown in text-fig. 11. *a-e* shows primary conterminant examples, as interpreted herein; *f-i* are secondarily conterminant hypostomes belonging to Libristoma; *j* may be secondarily conterminant (see discussion of Phacopida, p. 565). *a*, *Fieldaspis* (Corynexochida), Middle Cambrian (after Rasetti 1951, pl. 16, fig. 17), $\times 1.5$; *b*, *Palaeadotes* (Damesallacea), Cambrian, Mindyallan (after Öpik 1967, pl. 50, fig. 3), $\times 4$; *c*, illaenid (Illaenacea), Middle Ordovician (after Whittington 1963, pl. 18, fig. 4), $\times 3$; *d*, *Amphilichas* (Lichida), Middle Ordovician (after Tripp and Evitt 1981, pl. 2, fig. 28), $\times 6$; *e*, *Primaspis* (Odontopleurida), Silurian (after Chatterton and Perry 1983, pl. 5, fig. 5), $\times 6$; *f*, *Lycophron* (Asaphacea), early Ordovician (after Fortey and Shergold 1984, pl. 43, fig. 5), $\times 3$; *g*, *Remopleurides* (Remopleuridacea), Middle Ordovician (after Whittington 1959, pl. 17, fig. 18), $\times 6$; *h*, *Symphysurus* (Cyclopygacea), Middle Ordovician (after Fortey 1986, fig. 2), $\times 1$; *i*, *Degamella* (Cyclopygacea), early Ordovician (after Fortey and Owens 1987, fig. 38*d*), $\times 2.5$; *j*, *Salterocoryphe* (Calymenacea), Middle Ordovician (after Hammann 1983, pl. 11, fig. 107), $\times 6$.

doublure. Such derived hypostomal characters at once become of taxonomic use, in defining families, genera, or even species (asaphids are often best distinguished by hypostomal details). Hence, natant hypostomes are of a generalized type and change little; attached hypostomes are rapidly deployed into a variety of shapes and are as variable as any dorsal morphological features. This has to be connected with the function of the hypostome in the life habits of the trilobites included in the Libristoma.

If these facts are easily stated the possible explanations of the facts quickly become speculative. What is certain is that the natant condition was both widespread and enduring. As a derived character it was connected with life habits that the trilobites could ubiquitously and successfully prosecute from the Cambrian to the Carboniferous, and it is unlikely, therefore, that it was related to any peculiar specialization, such as parasitism. Because the hypostome remains remarkably conservative it is possible to suggest that it was not actively involved in the mastication of food, and this is supported by the lack of the kind of buttressed attachment found in the conterminant and impendent hypostomal conditions. So it seems reasonable to argue further that it was the very flexibility of the hypostomal attachment that was of adaptive importance. If Whittington's (1988*a*) view of the relationship between anterior hypostomal wings and anterior pits (or the homologous points in the axial furrows) is correct then the hypostome was tethered rather than entirely free-lying, but that the attachment was not rigid is shown by the ease with which it becomes displaced on death to produce specimens like that shown in Pl. 1, fig. 7.

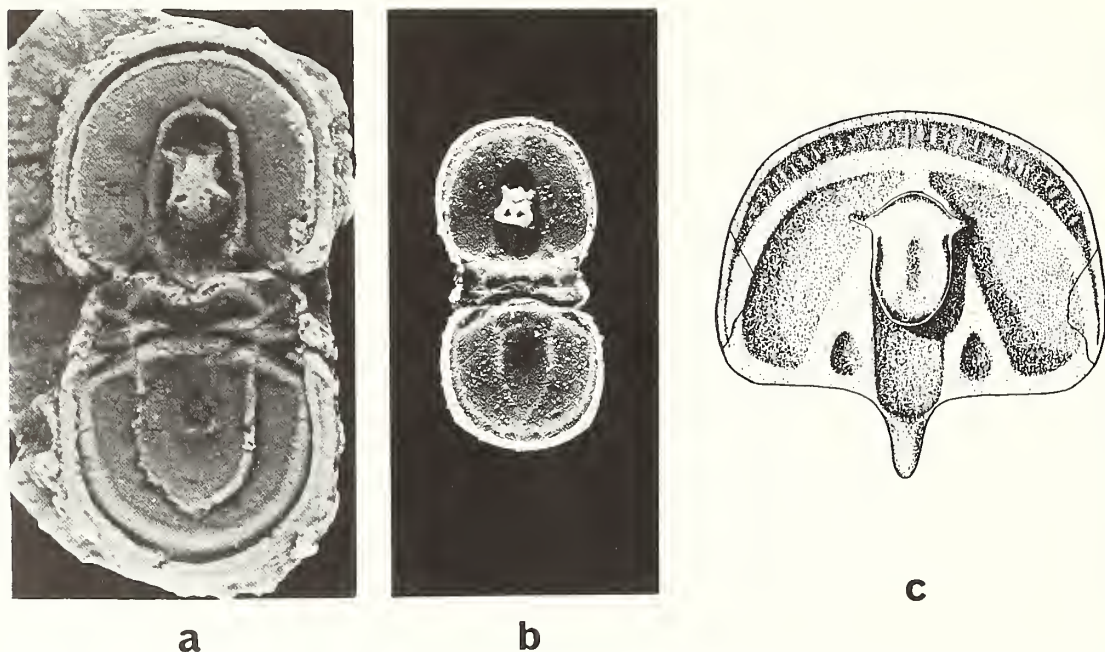
If the mouth lay at the back end of the hypostome it is not unreasonable to assume that the ovate middle body of the hypostome corresponded with some kind of foregut above it. In this case

flexibility of the hypostome would mean that the foregut might be manipulated by the hypostome itself. If we further assume that the hypostome was 'tethered' by the anterior wings this movement would be confined to up-and-down movement of the adoral margin: more precisely the movement would be upwards-and-backwards because of the tethering at the anterior end of the hypostome. It would be a scooping motion. The musculature necessary to do this would be appropriately sited if it attached to the middle furrows. It does not seem likely that the muscles were particularly powerful because the middle furrows are usually rather weakly defined. Hence it is likely that if the hypostome functioned in this scoop-like fashion the particles handled were small. This could either mean that the natant trilobite lived on small organic particles extracted from the sediment by the setate bases of the coxae (cf. Whittington and Almond 1987) and then passed forwards along the ventral 'food groove', or that the trilobite directly ingested partially sorted sediment, the process of nutrient extraction being carried out in the gut. In any case it seems unlikely that natant trilobites handled large prey. The scooping motion of the hypostome/foregut could have functioned in shovelling a considerable quantity of sediment and organic material for digestive processing. It may be relevant that many 'ptychoparioid' (Ptychopariidae, Olenidae, aphelaspids, etc.) trilobites have well-developed caecal networks, some of which have been interpreted as intestinal diverticulae (other workers claim these as arterial, see Jell 1974). But the conservatism of the natant hypostome attests to it not being directly involved with the manipulation and processing of food, however the food was derived.

As soon as the hypostome became secondarily conterminant or impendent specializations appeared. Whittington (1988*a, b*) has demonstrated that the hypostomes in all cases of conterminant or impendent attachment he examined were rigidly attached at the sutural junction with the doublure. This implies a functional difference compared with the natant condition. Such hypostomes cannot be involved with the shovelling of food forwards, but it becomes possible for them to become part of the mechanism of manipulating and processing the food gathered. The powerful buttressing of the hypostomal wings and doublure that happens in, for example, asaphids and nileids implies that mechanical strength was important in this function. Certain species with attached hypostomes have conspicuous rasps on the adoral part of the hypostomal margin: this is shown by the odontopleurids discussed by Chatterton and Perry (1985), and by the asaphid *Isotelus* (text-fig. 3*e*, p. 534). Such rasps could have functioned in concert with the limbs in the shredding or comminution of large food particles. It seems likely to me that the *Libristoma* having predatory habits were also those having secondary conterminant or impendent hypostomes. The specializations of the hypostomes were the result of the various stratagems evolved to deal with bulkier food items, including prey in at least some species. The function of rasps does not pose an interpretative problem, but many of the other specializations do. Forks, or lateral spine-like processes, are developed on many conterminant hypostomes, both primary and secondary (*Paradoxides*, calymenids, asaphids, some remopleuridids). In asaphids the fork extended to either side of the mouth and may carry strong terrace ridges on its outer surface (e.g. Fortey 1979, pl. 23, fig. 4) – could these have also helped in manipulating food? The maculae behind the middle furrows on asaphids and nileids are modified, bevelled areas, and their function is not resolved, but if the hypostomal retractor muscles remained they must have taken on a different function. Remopleuridids have enormously extended maculae the function of which is unknown. The spread of terrace ridges from the cephalic doublure onto the anterior part of the middle body of the hypostome in the secondarily attached condition means that this part of the hypostome has become, functionally speaking, part of the antero-venter. The function of terrace ridge systems in trilobites is not without controversy, but anterior cephalic ones probably functioned as sediment grippers in some instances (Schmalfuss 1981; Fortey 1986). In the secondarily conterminant families these changes from natant hypostome morphology happened over an early Ordovician period of perhaps ten million years. The functional interpretation of the specializations of attached hypostomes is a fruitful field for further research. For the moment it is only possible to contrast these morphological excursions with the conservatism of hypostomes separated from the doublure, for which one presumes a single function sufficed for several hundred million years.

CLASSIFICATION OF AGNOSTIDA

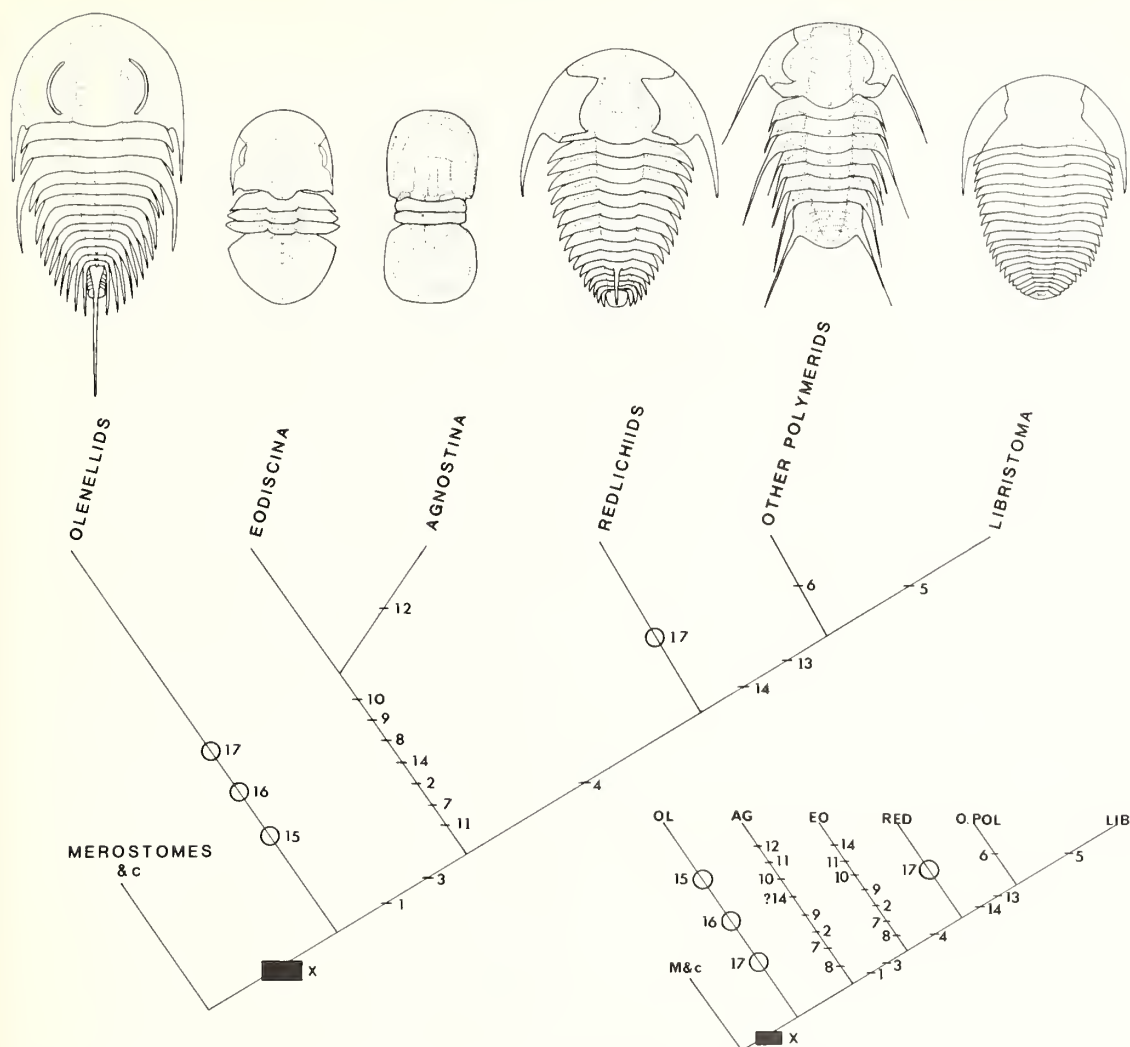
The Agnostida are usually understood to comprise the agnostids themselves, Suborder Agnostina, and the eodiscids and pagetiids (suborder Eodiscina *sensu* Moore (*in* Moore 1959); superfamily Eodiscoidea *sensu* Jell (1975)). There is now much evidence that the hypostome of the Agnostida was not attached ventrally (text-fig. 13). The apparently natant condition in Eodiscina has been discussed by Jell (1975, pl. 1, fig. 1) and Whittington (1988a), and is now known in several members of the Agnostina (Robison 1972a; Jell 1975, pl. 1, fig. 3; Müller and Walossek 1987; Robison 1988), and there is no reason to suppose it was other than general.



TEXT-FIG. 13. Natant hypostomal condition in Agnostida, showing no indication of rostrum. Agnostina: *a*, *Peronopsis ferox* (Tullberg) (Robison 1972a, fig. 2d) $\times 21$; *b*, *Onymagnostus seminula* (Whitehouse), (Robison 1982, pl. 4, fig. 5b), $\times 10$; photographs kindly supplied by R. A. Robison. Eodiscina: *c*, *Pagetia* cephalic shield from underside (after Jell 1980, pl. 1, fig. 1).

When I first recognized the natant condition as a synapomorphy I had considered that the agnostids should belong in the same monophyletic group as libristomates because of their unattached hypostome. This was wrong. The natant condition in Agnostida is **not** homologous with that in Libristoma. Recognition of this also serves to place the Agnostida within the Trilobita (text-fig. 14), which has been a long-standing problem. It is necessary to discuss this before considering the ptychoparioids further.

Much more is known of agnostid anatomy following Müller and Walossek's (1987) magnificent work. Obvious agnostoid specializations have led them to be classified separately from the rest of the Trilobita (Miomera of Jackel 1909). However, the original emphasis placed on the paucity of thoracic segments does not bear scrutiny because it is now known that several other groups of trilobites may include species with only two or three thoracic segments, for example *Corynexochida* (Robison and Campbell 1974) and *Raphiophoridae* (Zhang 1980). Small numbers of segments result from a change in developmental programme (cf. McNamara 1986), and it is not a character of great weight, taxonomically speaking, although it is stable in Agnostina. The fact remains that



TEXT-FIG. 14. Hypothesis of relationships placing Agnostida and Libristoma in the Trilobita as a whole. Smaller inset shows a second hypothesis which is not favoured by the author. The relationship of Libristoma to the group termed 'other polymerids' is not resolved. 'Other polymerids' comprises primary conterminant non-redlichiid trilobites: Corynexochida, Lichida, Odontopleurida, Scutelluina as discussed in text, and may not be a natural group. Derived characters are: X, combination of seven, possibly nine, synapomorphies of olenellids and other trilobites as discussed by Fortey and Whittington (1989) (presence of a pygidium; rostral plate; calcite eye lens structure; calcite cuticle; circum-ocular sutures in adult; eye ridges; hypostome with anterior wing directed dorsally to anterior pit; and possibly terrace ridges on doublure and spinose margin of larval hypostome); 1, acquisition of dorsal ecdysial sutures; 2, reduction in thoracic segment number to three or fewer; 3, acquisition of a calcified protaspis; 4, connective sutures present (section of doublure included on free cheek); 5, natant hypostomal condition; 6, glabella sharply truncated at ledge-like border; 7, loss of calcification of olenellid-like rostral plate; 8, occipital width greatly exceeds (tr.) width of preoccipital glabella (expressed as triangular 'basal lobes' in Agnostina); 9, broad, 'rolled' cephalic border; 10, cephalic shield long (sag.) (maximum width often in front of posterior margin); 11, genal spines reduced or absent; 12, cephalothoracic aperture; 13, protaspis/early meraspis eye ridges close to anterior margin ('ptychopariid style' protaspis); 14, fulcrum-and-facet thoracic articulation (flange-like articulation primitively present in olenellids and at least some redlichiids, position of acquisition of advanced articulation may be oversimplified here – probably accompanied by the capacity to enrol fully). Circles, some plesiomorphic characters: 15, dorsal sutures lacking; 16, rostral plate extending around ventral cephalic margin; 17, olenelloid glabella form (elongate, fusiform with round to acuminate frontal lobe). The illustrated genera are only token representatives of their groups, and not necessarily those from which coding was made.

the Agnostina are the most specialized of trilobites, possibly being planktic (Robison 1972*b*) and spending much of their life in the enrolled condition, according to Müller and Walossek (1987). This is not, however, relevant to their classification within the trilobites, which has to be based on shared characters rather than distinctive autapomorphies. Their peculiarities have tended to dominate the view about how they should be classified, for example: they 'are best treated within the Trilobita at present but...having a separate position within them' (Müller and Walossek 1987, p. 54).

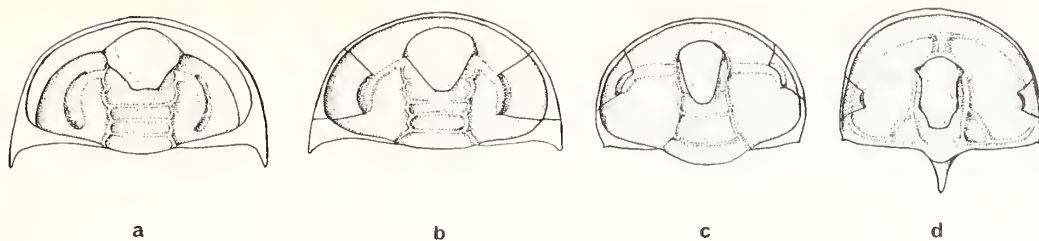
The relationships of the Agnostida suggested here are shown on the cladogram (text-fig. 14). This places them firmly within the Trilobita, between the Olenellida and Redlichiida. If the reasons advanced by Fortey and Whittington (1989) for the olenelloids as the most primitive trilobites are accepted, this is the preferred position for the agnostoids based on the characters I consider relevant to the problem.

The reasons for this phylogenetic position are threefold:

1. Students of Eodiscina agree that this group is related to Agnostina, of which they may be the primitive sister group (Jell 1975; Zhang *et al.* 1980). According to Zhang *et al.* (1980, text-fig. 7) two different groups of agnostids may have been closely related to different eodiscids – implying that the latter is a paraphyletic group and the former polyphyletic. However these relationships are worked out in detail, within the Eodiscina as understood at present there appear to be a series of 'intermediates' spanning some of the gaps between pagetiid organization and agnostid organization: three and two segmented species within the same genus (*Pagetia* as discussed by Jell 1975); blind eodiscids otherwise with pagetiid features (see Rasetti 1966); and some eodiscids with pre-occipital median tubercles on the glabella (*Serrodiscus* and *Ladadiscus*, see Rushton 1966, text-figs. 3, 9). The agnostid hypostome is so far unique in construction (Robison 1972*a*) with its window-like openings, although according to Müller and Walossek (1987) this may only be a matter of cuticular thinning (see also Robison 1988, fig. 9). The cephalothoracic aperture (a gap between the thoracic axis and cephalon in the enrolled state produced by the absence of the articulating half-ring on the first thoracic segment) is considered to be a good apomorphic character of Agnostina. The hypostome of *Pagetia* is no different from the generalized 'ptychoparioid' hypostomes shown on text-fig. 11 (Jell 1975, pl. 28, figs. 1 and 2). Hence, for comparative purposes, the most primitive pagetiids are probably the best candidates for comparison with other trilobites to determine the relationships of Agnostida. They have dorsal facial sutures. The presence of such sutures was considered by Fortey and Whittington (1989) to define a clade of 'higher' (i.e. non-olenelloid) trilobites, and most authors agree (Bergström 1973; Lauterbach 1980) on the peculiarity of this character in arthropod phylogeny.

2. Redlichiida, and all other trilobites, other than olenelloids and Agnostida, have a rostral plate bounded laterally by connective sutures – or if the rostral plate has been lost (e.g. to produce fused cheeks) it is known that their ancestors had such a rostral plate. In ventral view free cheeks of this group show a truncated section of doublure. Olenelloids have a broad crescentic rostral plate, without connective sutures. If the olenelloids, on other criteria, are the most primitive trilobites, this form of rostral plate is also primitive. Ventral-side up preservation of numerous Agnostida, including those with hypostomes in place (text-fig. 13), show no sign of a rostral plate. The primitive agnostoids with dorsal sutures included in Pagetiidae do not show that part of the genal doublure bounded by connective sutures. Hence, the rostral form must have been as in olenelloids, but calcification has been lost (text-fig. 15). This is confirmed by an example where it appears to have been silicified in one of the youngest agnostids (Middle Ordovician, Hunt 1966), but still retains olenelloid form. The loss of calcification of the (olenelloid) rostral plate affords an autapomorphy defining the Agnostida, one which is unique in the Trilobita.

3. It follows that the unattached condition of the hypostome in the Agnostida is the result of loss of the rostral plate and not the same as in the Libristoma. Individual agnostoid ontogenies described by Jell (1975) and Rushton (1966) show that the preglabellar field became progressively longer during ontogeny. It is suggested that the most primitive member of the Eodiscina could be such a species as *Sinodiscus changyanensis* S. G. Zhang in Zhang *et al.*, 1980, in which dorsal furrows and eye ridges are well-defined (as in olenellids) and the preglabellar field is short.



TEXT-FIG. 15. Series of cephalic shields viewed from the ventral side to illustrate why natant condition in Agnostida is not homologous with that in Libristoma, and, left to right, morphological steps in origin of Agnostida. Only *b* is hypothetical. *a*, primitive condition illustrated by typical conterminant olenellid (*Holmia*, see Whittington 1988a) showing long crescentic rostral form, confining other cephalic doublure to narrow selvage; *b*, dorsal sutures have appeared, but calcified rostral plate lost; *c*, most primitive kind of pagetioid (well-defined glabellar furrows, glabella extends comparatively far forwards) based on *Sinodiscus* (Zhang *et al.* 1980, pl. 4, figs. 16–21); *d*, *Pagetia* (based on Whittington 1988a) illustrating advanced agnostoid morphology triangular 'basal lobes' (possibly extraglabellar) and glabella further short of cranial margin.

Another character may be cited in the question of agnostid relationships. No protaspis has been described for an olenellid (Palmer 1957), nor yet for a member of the Agnostina. Since meraspides are well known for both it seems likely that this is a consequence of calcification not having 'spread back' far enough in ontogeny in these groups, which again would be interpreted here as a primitive feature. However, given the other specializations of agnostids, lack of protaspis could well be a secondary loss. J. H. Shergold informs me that he has found an eodiscoid protaspis (Zhang 1989; Hu 1971, pl. 7, fig. 23), which would confirm the latter view. Planktic ostracodes, resembling agnostids in size and putative life habits, undergo accelerated development in the egg stage, and of all the ostracodes only one genus, *Manawa*, has a free-living nauplius larva (Swanson 1989). An alternative view might separate Eodiscina and Agnostina as distinct clades, influenced perhaps by the more general 'ptychoparioid' appearance of the former, is shown also on text-fig. 14. This produces a less parsimonious arrangement of the characters I consider important, and is not favoured.

If these characters are interpreted correctly the Agnostida appear above the olenelloids by virtue of their (primitively present) dorsal sutures but below all other trilobites, including Libristoma, because they had not acquired the advanced rostral form. This position does justify their high taxonomic status, and is also consistent with their early stratigraphic appearance in the Lower Cambrian of, for example, China. The loss of calcification of the crescentic rostral plate is one character (and perhaps the most important) defining Agnostida. They are not part of Libristoma.

DIAGNOSIS AND STATUS OF LIBRISTOMA

The Libristoma may be diagnosed as follows: *Trilobites having natant hypostomal condition, or with secondarily conterminant or independent hypostomal condition.* Rostral plate bounded by connective sutures primitively present, but may be lost by virtue of fusion of the free cheeks, or replaced by median suture.

If Libristoma is a high level monophyletic taxon then it requires taxonomic recognition. A glance at Harrington's (*in* Moore 1959) review of high level trilobite taxonomy quickly shows that the fate of most of the proposed high level taxa in the past has been oblivion. Few authors use such orders as Miomera, Epiparia, Polymera or Protoparia at the moment, and none of these is equivalent to Libristoma. Miomera and Polymera are occasionally employed by Cambrian specialists (Robison 1988); Miomera is equivalent to Agnostida as used here, while Polymera is an unnatural taxon used to encompass the rest of the non-agnostid trilobites. In dealing taxonomically with the new phylogenetic concept implied by Libristoma there were two choices.

1. To redefine the Order Ptychopariida to equate with Libristoma. This would mean that major

monophyletic taxa within the redefined ptychopariids would become suborders. This would include Proetida, which has been regarded as a separate order, although Lütke (1980) regarded Proetida as a ptychopariid suborder. Also, for reasons explained below, the suborder Ptychopariina resulting from this classification would be paraphyletic, and it is perhaps wiser to provide a clear nomenclatorial distinction between an allegedly monophyletic group (libristomates as a whole) and its least satisfactory subgroup.

2. To propose Libristoma as a Subclass. In this case the major groups within Libristoma can be regarded as Orders, which does least violence to the existing classification. This runs the risk that Libristoma, like the major subdivisions proposed in the past, will simply not be used. On the other hand, if it is a good monophyletic taxon it should survive by virtue of the light it casts on major phylogenetic events in trilobite history. The trouble with, say, Stormer's (1942) Order Proparia (including eodiscids, norwoodiids, burlingiids and Phacopida on the basis of proparian facial sutures) was not so much the high level status of the taxon involved as the fact that it has subsequently been proved to be a polyphyletic assemblage.

For the moment I prefer the second option. A stricter cladist would insist that a full phylogenetic analysis of the whole group be carried out before the question of taxonomic status is decided. I accept that this kind of study may alter the status of the subgroups within Libristoma. For the moment a pragmatic option is to retain major monophyletic subgroups of Subclass Libristoma as Orders or Suborders, which is what is done below. Suborders are retained within Ptychopariida for no better reason than traditional usage, and this may well change in the future.

Orders and suborders within Libristoma and their diagnoses

The subgroups within Subclass Libristoma should be definable on autapomorphies, with the natant hypostomal condition being the synapomorphy uniting the whole group. A list of primitive characters within the accepted 'Ptychopariida' was given by Fortey and Chatterton (1988, table 2). These include: rostral plate present (transverse width not exceeding that of glabella); tapering glabella with three pairs of glabellar furrows which are shorter anteriorly; a relatively large number of thoracic segments with unspecialized articulation; opisthoparian sutures; terrace ridges on doublure; genal spines present; unspecialized hypostome of the kind discussed above. Most of these characters are present also in redlichiids and are therefore simply characters of all trilobites of the Redlichiid + Libristoma clade: for example, genal spines; opisthoparian sutures; large numbers of thoracic segments; larval hypostomal margin with fringe of spines; glabellar form in many species of redlichiid; terrace ridges on doublure (Kobayashi and Kato 1951, pl. 5, fig. 6; Hupé 1953, pl. 9, fig. 9). With the exception of opisthoparian sutures and the glabellar form, most of these characters are also present in olenellids, and if the olenellids are regarded as trilobites, such characters are simply generalized characters of the trilobites as a whole (Fortey and Whittington 1989). So diagnostic characters of subgroups of Libristoma must comprise characters outside this list.

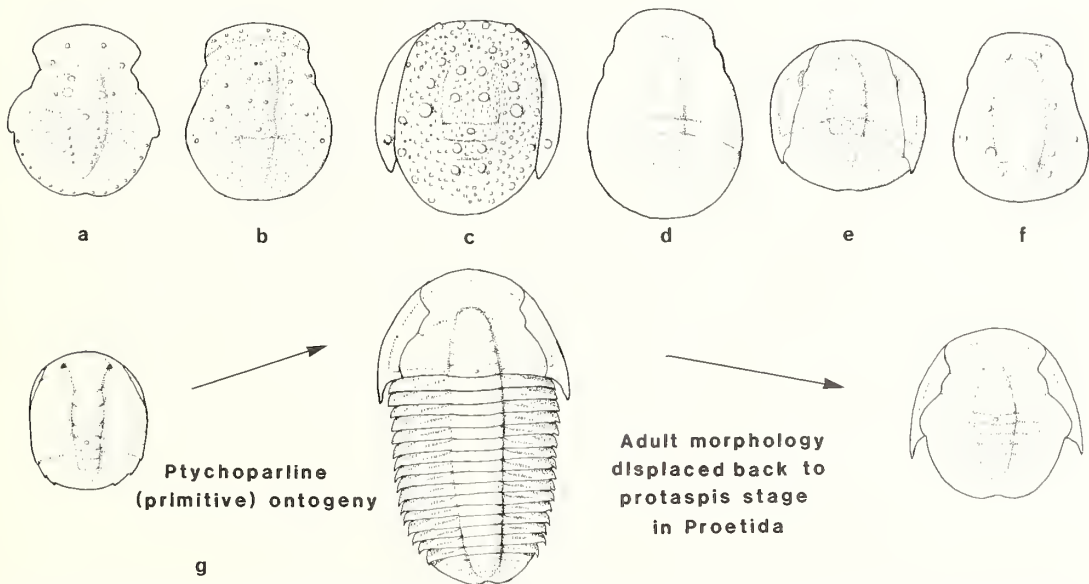
Order PROETIDA Fortey and Owens, 1975

Diagnosis. Libristoma having fusiform glabella in the protaspis stage, and natant hypostomal condition attained early in ontogeny. Larval hypostome margin lacking spines. Most species natant also in adult; some secondarily conterminant or impendent. Median occipital tubercle usually present.

Fortey and Owens (1975) proposed Proetida for what they regarded as a major natural group of trilobites which had been incorrectly classified in the *Treatise* (Moore 1959). Despite the criticisms of Bergström (1977) Proetida has gained wide acceptance since, and some additional taxa have been added to the group (e.g. Telephiniidae by Chatterton 1980). Lütke (1980) recognized the group as a suborder of Ptychopariida, and therefore part of the 'ptychopariid problem'. Fortey and Owens' original list of attributes of Proetida was based on what they regarded as overall similarity of the taxa included, without critical assessment of what characters were plesiomorphic and what derived. Part of their argument for monophyly stemmed from a stratigraphical/morphological hypothesis that all Proetida could be derived from the early Ordovician

Hystricurinae. Now that it has been recognized that the majority of Proetida (and all primitive ones) had natant hypostomal condition it is possible to apply a more critical judgement to the characters on which the group is based. If it is a natural group there should be a synapomorphy defining it, whether or not the hypothesis of hystricurine derivation is correct. Many of the proetide characters Fortey and Owens listed (1975, pp. 235–6) are generalized 'ptychopariid' (cf. Fortey and Chatterton 1988, table 2) or even belong to the whole Libristoma: they will not suffice for the definition of the group. Bergström's (1977) criticisms were justified on this point. For example, the hypostomal form described by Fortey and Owens is simply that of the typical natant trilobite (text-fig. 11), while the presence of terrace ridges on the doublure is an even more symplesiomorphic character, being present in Redlichiida and even Olenellida also.

Fortunately for the concept of Proetida there *is* a derived character uniting the group, but this does not become apparent until the hypostomal condition is brought into the argument. Fortey and Owens (1975) did point out that early growth stages of Proetida resembled one another, and illustrated early meraspid cranidia of various families showing tapering, rather elongate glabella with a deeply parabolic outline. A preglabellar field was present even at this early growth stage. Chatterton (1980) and Fortey and Chatterton (1988) noted the similarity of proetide protaspides. These differ from the typical 'ptychopariid' (text-figs. 9 and 10) in having a fusiform, anteriorly rounded or pointed glabella. That this is general for the Proetida is demonstrated (text-fig. 16) by the occurrence of proetide type protaspides in Proetidae (*Proetus*, see Chatterton 1971, pl. 16, fig. 1), Bathyuridae (*Licnocephala*, see Ross 1953; *Bathyurus*, see Chatterton 1980), Aulacopleuridae (*Harpidella*, see Chatterton 1971, pl. 18, fig. 20; *Scharyia*, see Šnajdr 1981), Dimeropygidae (*Dimeropyge*, see Tripp and Evitt 1983), and Telephinidae (*Phorocephala* (*Carrickia*), see Chatterton 1980; also *Carolinites*, see Fortey 1975, pl. 36, figs. 12–15 meraspides). It is reasonable to assume that the proetide protaspis type was present throughout the group.



TEXT-FIG. 16. Late protaspides of various families within Proetida to show synapomorphy of tapering glabella (which falls short of border in these late protaspides); compare text-fig. 10 h–m. a, *Scharyia* (Scharyiinae; Aulacopleuridae) (after Šnajdr 1980, text-fig. 1d), $\times 20$; b, *Phorocephala* (Telephinidae) (after Chatterton 1980, fig. 5), $\times 40$; c, *Dimeropyge* (Dimeropygidae) (after Tripp and Evitt 1983, pl. 31, figs. 16–21), $\times 40$; d, *Bathyurus* (Bathyuridae) (after Chatterton 1980, fig. 5, and pl. 6, fig. 4), $\times 25$; e, *Proetus* (Proetidae) (after Chatterton 1971, fig. 15c and d), $\times 20$; f, *Aulacopleura*? (Aulacopleurinae; Aulacopleuridae) (after Hu 1971, pl. 23, fig. 8; note: Hu assigned the species from which this protaspis is taken to the Proetidae and the genus *Phaseolops*; it seems to the writer far more likely to be an aulacopleurid; also Hu's drawing of the protaspides (his text-fig. 53a–d) misinterprets the glabellar shape, and the illustration here is based on the photograph cited). g, heterochronic hypothesis for the origin of the proetide type protaspis from the conventional libristomate development (see text-fig. 9).

Because the protoglabella in this kind of protaspis falls somewhat short of the border the proto-hypostome corresponding with the forward part of the glabella must lie a little to the posterior when compared with the ptychoparioid protaspis. At the smallest protaspis stages (at which the rostral plate has not yet developed) Tripp and Evitt (1983) show the proto-hypostome attached to the doublure in *Dimeropyge*, and Chatterton (1971) has indicated that the same applied to the earliest proetid growth stages. Šnajdr's (1981) full ontogeny of *Scharyia* shows that the preglabellar field lengthens during protaspis ontogeny. By the earliest meraspis the cranial border is clearly developed and Šnajdr's plate 2, fig. 7 also shows that the genal doublure is both coincident with the border, and much narrower (sag.) than the preglabellar field separating the tapering glabella from the border. The hypostomal condition must have been natant. The same argument can be repeated for the meraspis cranidia of the Proetida shown in Fortey and Owens (1975, fig. 3), spanning most of the proetide families. A full ontogeny of hystricurids is not described, but a very small cranidium of *Parahystricurus oculirotundus* Ross (1951, pl. 12, fig. 33) shows identical features, and, because the cephalic doublure is known to be narrow in that species, it is likely that the early onset of the natant hypostomal condition applied also to the hystricurids. It is possible that the natant condition extended even into the protaspis in *Scharyia*, which has a wide area in front of the proto-glabella from the earliest protaspis stage. The spinose margin of the larval hypostome is a character shared by almost all trilobites (Fortey and Whittington 1989), and could be argued to be a synapomorphy of the whole group. But in Proetida for which larval hypostomes have been described (e.g. *Proetus*, see Fortey and Chatterton 1988, fig. 13; *Dimeropyge*, see Tripp and Evitt 1983) the spinose margin is apparently lacking. In this respect these larval hypostomes are more like that of the adult, and differ from immature hypostomes of all other trilobites.

The Proetida can thus be defined within the Libristoma by their protaspis type, and by the 'displacement back' of the natant hypostomal condition, and probably the non-spinose hypostomal margin, into early ontogeny. Because some stratigraphically late Proetida (above) become secondarily conterminant and impendent it is likely that there were reversals (i.e. natant to conterminant) in the ontogeny of such forms, but because they are undisputed proetids this does not pose a problem for the definition of the group as a whole. What is less certain is whether the neat 'cut-off' at the Cambrian-Ordovician boundary suggested by Fortey and Owens (1975) applies with the definition of the Order given here. Fortey and Owens based their stratigraphic definition of the group on the hypothesis that Proetida were all derived from hystricurines. While this is reasonable for dimeropygids and bathyurids (and probably telephinids) for which there are a series of intergrading species between hystricurids and the derived families, this is much less clear for proetids and aulacopleurids. It now seems perfectly possible that one or more Upper Cambrian families will prove to have a proetide protaspis – and if this is the case they, too, should be assigned to Proetida. Solenopleuridae is an obvious candidate; some Cambrian solenopleurids seem to me indistinguishable from Ordovician *Hystricurus*. Ontogenetic studies on trilobites in the later Cambrian, or even the mid Cambrian, might well reveal an extension of Proetida from its present post-Cambrian assemblage of families. Dimeropygidae are better placed in the superfamily Bathyuracea, rather than in Proetacea as in the 1959 *Treatise*.

Order ASAPHIDA Salter, 1864, emend. Fortey and Chatterton, 1988

Diagnosis. Libristoma having ventral median suture. Only primitive forms retain natant hypostomal condition, the majority of the group being conterminant or impendent. Higher Asaphida also have a distinctive inflated protaspis – the asaphoid protaspis.

This major group was defined at length by Fortey and Chatterton (1988) to which paper the reader is referred for details. It was treated as a suborder there, pending further discussion of the ptychopariid problem. If the concept of the Libristoma is accepted its rank can be elevated to Order as discussed previously. Shergold and Szűcs (1984) have already employed Asaphida as an order, although with a more restricted view of what trilobite groups should be placed within it than that of Fortey and Chatterton (1988). The superfamilies Anomocaracea, Asaphacea (incorporating Ceratopygacea), Remopleuridacea, Dikelocephalacea, and Trinucleacea were included in Asaphida in that work, together with a number of additional families, such as Pterocephaliidae and Dikelocephalinidae. To this list can be added the family Parabolinoidea. Westrop (1986) has recently described a ventral median suture for this group, and because this is the main synapomorphy of Asaphida this is where the family belongs unless it can be shown that the median suture was independently derived therein. Parabolinoidea are interesting in that the bulk of their morphology is almost an inventory of primitive and generalized ptychoparioid characters (Fortey and Chatterton 1988, table 2). As Westrop has pointed out they resemble olenids in many features – but we know that olenids were derived from

ptychoparioids with a rostral plate, not a median suture, and on our analysis of the characters, therefore, such resemblances are because of symplesiomorphies, and misleading.

The placing of Asaphida within the larger group Libristoma is proved by the apparently universal occurrence of the natant hypostomal condition in the primitive members of the group, which are also the stratigraphically earliest. These include the families Anomocaridae, Auritamiidae, Pterocephaliidae, Parabolinoidea, listed above, and probably Liostracinidae (Fortey and Chatterton 1988, p. 879). For the moment these have been retained in a paraphyletic group Anomocaracea – based on the retention of the natant condition in combination with the median suture – but further analysis should ally these families with one or another of the derived monophyletic groups.

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder OLENINA Burmeister, 1843

Diagnosis. Ptychopariida with thin dorsal exoskeleton; free cheeks yoked together as single unit connected by narrow (sag.) doublure (rostral plate present only in the most primitive members of *Olenus*).

Olenids comprise an accepted monophyletic group (Henningsmoen 1957). Most occurred in dysaerobic palaeoenvironments. Probably more than in any other trilobite group many relationships within the olenids have been determined stratigraphically, especially because of the work of Westergård, Henningsmoen and Kaufmann in Scandinavia. This is possible because their record in the Upper Cambrian 'olenidskiffer' is exceptionally continuous. I see no reason to doubt the phylogenies resulting from this work, even though it has to be said that subfamily relationships are not clear. It is a paradox that the very completeness of the olenid phylogenetic history has probably hindered phylogenetic study of other Cambrian groups. The olenid model dictates that if enough collections are made and enough stratigraphy is done the phylogeny will simply 'fall out' from sequence, allowing a direct reconstruction of the historical tree of descent. However the bulk of the olenids occupied a distinct, stable and peculiar environment, certainly dysaerobic and possibly beneath the thermocline (Fortey 1974; Cook and Taylor 1975), which favours the preservation of a continuous phyletic succession of species. This does not apply to the greater part of the shelf record, nor even to deeper environments in which oxygenation was normal.

As Henningsmoen (1957) noted, the morphological excursions taken by olenids in their long Cambro-Ordovician history makes the framing of a diagnosis very difficult. I introduced the fused free cheeks into the diagnosis (Fortey 1974) and this has been subsequently adopted also by Nikolaisen and Henningsmoen (1985). This fusion is true of all olenids for which the material is adequate to see it, other than the earliest species of *Olenus*, which still have the rostral plate. These species of *Olenus* form the sister group of the rest of the Olenidae. Because they include the type species *O. gibbosus* (Wahlenberg) it is obviously necessary to 'draw the line' for the family below these species. An important point is that the fused cheeks of olenids are not homologous with those of Asaphida which develop them (Kainellidae, Nileidae and Cyclopygidae) because they result from the loss of a rostral plate, not a median suture. All olenids except possibly the stratigraphically youngest *Triarthrus* (Whittington and Almond 1987) apparently retain the natant hypostomal condition, but it would not be surprising to find other examples of secondary conterminant hypostomal condition among pelturines with reduced preglabellar fields. In any case (cf. Nikolaisen and Henningsmoen 1985) one cannot incorporate the natant condition into the diagnosis as it is the general character of Libristoma.

There is now the greater problem of whether families other than Olenidae can be assigned to Olenina. Various attempts have been made in this direction. One problem is that unrelated trilobites may have 'olenimorph' features (such as numerous narrow thoracic segments with wide pleurae, long genal spines, caecate dorsal surface) because they, too, became adapted to the dysaerobic environment. Good examples would be *Hedinaspis* among the Asaphacea, *Aulacopleura* among Proetida, *Seleneceme* among Trinucleacea. In the *Treatise* (Poulsen in Moore 1959) the family Papyriaspidae was included; as we have noted above there is no evidence to support this, apart from generalized ptychopariid similarity. Palmer (1965) has stated that *Aphelaspis*, which is not a pterocephaliid, might be related to Olenidae. Shergold (1980) included Elviniidae in Olenacea. Westrop (1986) included not only this family, but Idahoiidae, Parabolinoidea, and Pterocephaliidae in the same superfamily. In the analysis of Fortey and Chatterton (1988) these last three would be part of Asaphida, having a median suture. The problem is that I can find no synapomorphic characters to link any of these families to Olenidae in particular. The characters they share are all those of primitive ptychopariids. Westrop (1986) states that he followed Ludvigsen and Westrop (1983) in the reasons for associating his selection of families with Olenidae, but in the latter paper there are no characters listed that

might unite such a group. One has to conclude that the association is made on 'general' resemblance and on the stratigraphic presumption that they are all similar enough in age to be likely to constitute a natural group. Obviously Olenidae had to have a sister group, and I am certain that a major libristomate group including the olenids will be recognizable. At the moment I can see no characters to define such a group. For this reason Olenina are retained as a suborder of Ptychopariida *faux de mieux*. I think it wiser to restrict the scope of Olenina to a genuinely monophyletic group, rather than cram in other families on spurious grounds with the risk of creating a polyphyletic taxon.

Suborder HARPINA Whittington, 1959

Diagnosis. Libristoma having small eyes placed anteriorly relative to glabella; cephalon broadly convex (sag. tr.) with long preglabellar area, and often a brim, with stout genal spines or genal prolongations of the brim; free cheeks narrow (tr.) or lost altogether, fused together; thoracic segments numerous (12 or more) and characteristically narrow (sag.) with long pleurae in contact along their length; pygidium relatively small and often transverse.

The natant condition of the hypostome of *Harpides* is clearly illustrated on the holotype of the type species illustrated by Barrande (1872), and was suggested for Harpetidae by Whittington (1988*b*, p. 328); I know of no harpinid in which the hypostome has become secondarily conterminant. Even the earliest harpidinids (which are found at an horizon close to the Cambrian-Ordovician boundary) are specialized in most respects. There is no better hypothesis available for their Cambrian ancestry than that they are related to the Upper Cambrian to early Ordovician genera *Loganopeltis* and *Loganopeltoides*. *Loganopeltoides* still has narrow free cheeks, defined by sutures which are subparallel and close (Rasetti 1945). Rasetti (1948) demonstrated how a harpid-like cephalon could result from 'closure' of these sutures leaving the eyes isolated within the genal fields, a situation seen in the *Harpides*-like genus *Loganopeltis*.

All Harpina have the doublure fused as a single piece, as do loganopeltids and entomaspids (Rasetti 1952*b*; Ludvigsen 1982) which were placed in Harpina in Moore (1959). However, if the Harpina belong within the Libristoma the ancestor from which the group derived presumably carried a rostral plate, which was lost in the same fashion as in Olenina. At some stage also there must have been a change from a normal opisthoparian facial sutures. Ludvigsen (1982) assigned the genera *Heterocaryon* and *Bowmania* to Entomaspidae, both of which have normal opisthoparian sutures. He also placed the Entomaspidae in the superfamily Solenopleuracea, and hence presumably regarded them as unrelated to Harpina. If this were the case then presumably the harpinid features of entomaspids would have to be evolved in parallel, which would be hard to prove because Solenopleuracea has no autapomorphies. Ludvigsen also drew attention to the resemblance between entomaspids and the older genus *Doremataspis* Öpik, 1967 – which Öpik placed in another superfamily, Liostracinacea. This is some measure of the confusion pertaining in Cambrian trilobite classification. It is worth mentioning that there are some similarities also between Harpina and the mostly Upper Cambrian Superfamily Norwoodiacea: anterior position of small eyes, stout genal prolongations, wide and flat thoracic pleurae, and a tendency for the reduction of free cheeks (*Norwoodia* has strongly proparian sutures which have become almost parallel in the fashion of *Loganopeltoides*). Again, homoplasy will no doubt be invoked to explain these similarities. The best that can be said is that the Harpina have no recognized sister group, and to follow existing usage in retaining it as a suborder of Ptychopariida.

Suborder PTYCHOPARIINA Swinnerton, 1915

Diagnosis. A paraphyletic libristomate group retaining primitive characters; a combination of: relatively narrow rostral plate present, glabella barrel-shaped to tapering; natant hypostomal condition (possibly some secondarily conterminant); hypostome unspecialized; protaspis with forward-expanding axis reaching far forwards; with few exceptions micro- to heteropygous.

It is now possible to return to the 'ptychopariid problem' in the context of the recognition of the monophyletic groups listed previously. Having 'hived off' these natural groups there remain a collection of families which do not have the derived characters typifying these groups (or in which such characters are not known because of the poor state of knowledge of the ventral sutures and/or ontogeny of the group). What characters there are are often those of *Ptychoparia* itself, and primitive for Libristoma as a whole. Because we *cannot* yet assign such trilobites as more closely related to one or another of the derived groups there is little choice but to retain

a Suborder Ptychopariina for their reception. Because they include the primitive libristomates they are considered here to have descended from a common ancestor; because they also will include the sister taxa of Proetida, Olenina, Asaphida, and presumably Harpina, the Ptychopariina constitutes a paraphyletic assemblage. Ptychopariina can only be defined as being libristomate, but not having one or another of the synapomorphies that define the monophyletic Orders or Suborders. This is scarcely satisfactory, and to a strict cladist not acceptable at all. I would regard it only as a convention to accommodate primitive libristomates until they can be related to one or another of the derived groups. Before this can be done, I believe more characters will have to be brought into play than I have considered in this paper.

Such a concept of the Suborder Ptychopariina would result in the inclusion of the following superfamilies (uncritically culled from Moore 1959): at least some Ellipsocephalacea (transferred from Redlichiida, see above); Ptychopariacea; Conocoryphacea; Crepicephalacea; Illaenuracea; Solenopleuracea; Asaphiscacea; Komaspidae (excluding Telephinidae which are Proetida); Raymondinacea; Norwoodiacea (unless they prove to belong in the Harpina); and Marjumiacea. Some groups included in Ptychopariida in the *Treatise* (Moore 1959) would be excluded because they were probably not natant, especially Leiostegiacea and Damesellacea. I return to these below.

One can be critical of almost all the superfamilies of Ptychopariina as natural groups, and this has been reflected in a reluctance to employ these higher categories by more cautious authors such as Robison (1971) and Zhang and Jell (1987). The whole group needs proper phylogenetic analysis. It can be noted that:

1. Conocoryphacea is almost certainly polyphyletic (contrast Eldredge 1977). The uniting character is loss of eyes. This character is known to be derived many times in the history of the trilobites, for example, in Proetida, Phacopida, Trinucleacea and Agnostina. A comparison of the contrasting glabellar structures of such conocoryphacean genera as *Bailiella*, *Conocoryphe*, *Hospes*, *Hartshillia* and *Shumardia*, shows that they are more likely to be more closely related to disparate (but eye-bearing) ptychopariids than to one another. For example, *Bailiaspis* might be related to *Solenopleura*, *Conocoryphe* to *Ptychoparia*, on the basis of their cephalic morphology. The conocoryphaceans do not even 'lose' the eyes in the same way: *Bailiella* has short, 'marooned' eye ridges and comparatively wide fixed cheeks, while *Conocoryphe* and *Meneviella* have long genal ridges and marginal sutures. The Conocoryphacea has simply been used as a taxon to collect together blind ptychopariids which are merely the result of (especially Middle Cambrian) adaptations to off- or outer-shelf atheloptic situations.

2. It is scarcely possible to produce a differential diagnosis of Ptychopariacea, Solenopleuracea and Marjumiacea which presumably should be possible if any one of them is a natural group. As it is, they encompass only primitive ptychoparioid morphologies.

3. Illaenuracea and Raymondinacea are strikingly heterogeneous groups, which are not definable; some of the families within these groups have already been reassigned (e.g. by Westrop 1986), and the coherence of those remaining is in doubt.

4. Komaspidae and Norwoodiacea are probably natural groups, but as with the Olenina their sister group relationships are uncertain.

These problems are enough to show that we have no idea at present on how to dismantle the Ptychopariina as a paraphyletic group, even with the restriction on the definition of the group I have introduced in this paper. Further stratigraphical studies may allow for the recognition of monophyletic subgroups, but if the lack of success in the past is any guide, it seems most unlikely that stratigraphic series will do more than resolve a few generic relationships, leaving the broader issues untouched. The future seems to me to lie in the recognition of monophyletic groups, and the recognition of their sister groups within the Ptychopariina, which will allow those groups to be 'hived off' into the derived group (similar to the way in which Fortey and Chatterton (1988) placed the 'ptychoparioid' anomocaraceans into the Asaphida). Even so there will probably remain a core of ptychopariids sharing only the primitive grade of libristomate organisation, and differing only in characters of the most trivial kind (see, for example, the ptychopariid subfamily Antagminae, Rasetti *in* Moore 1959, p. 236). These will likely remain classified together, as perhaps they should.

CLASSIFICATION OF TRILOBITE GROUPS FORMERLY REGARDED AS PTYCHOPARIIDS

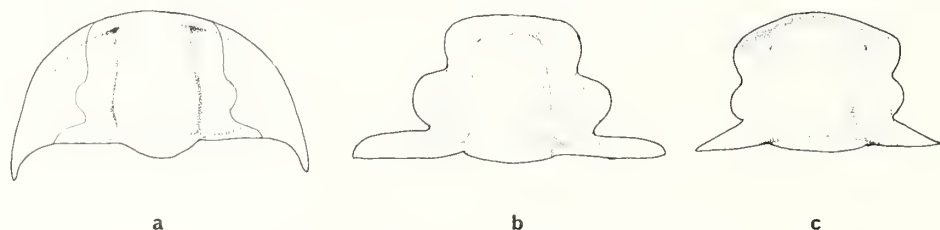
If it is correct to regard the Libristoma as a monophyletic group, trilobites which do not have natant hypostomal condition (or did not have a natant ancestor) are classified elsewhere. They are not part of the 'ptychopariid problem' except insofar as they have been classified with Ptychopariida in the past. This applies to the following superfamilies in the 1959 *Treatise*: Damesellacea, Leiostegiacea

(including Tsinaniidae), Illaenacea (which excludes proetids and relatives) and Calymenacea by virtue of their supposed ptychopariid origins. The important question about non-natant groups where their ancestry is uncertain is whether they were primitively conterminant or whether they were secondarily so, having been derived from a natant ancestor in the manner of most Asaphina. Unless there is evidence to the contrary it is reasonable to assume that they were primarily conterminant, this being, of course, the primitive condition. This assumption may not prove to be justified, especially with regard to the Phacopida.

The superfamilies removed from Ptychopariida (*sensu* 1959 *Treatise*) can be accommodated within other non-libristomate groups, as follows. Detailed evidence will be reviewed elsewhere.

1. *Superfamily Illaenacea*. The families Illaenidae, Styginidae (= Scutelluinae) and Phillipsinellidae belong in a monophyletic group termed the suborder Scutelluina (emend. from Superfamily Scutelloidea Hupé, 1953) by Lane and Thomas (1983), for which I retain the older name Illaenacea. This may be part of a larger group to be included within the Order Corynexochida, as noted by Přibyl and Vanek (1971). Corynexochida is usually considered to be Cambrian, and inclusion of Illaenacea would extend its stratigraphical scope to the Devonian.

2. *Superfamily Leiostegiacea*. With the inclusion of *Annamitella* in the Leiostegiacea (Fortey and Shergold 1984) the range of this superfamily extends from the Cambrian until well into the Middle Ordovician. Few articulated leiostegiaceans are known and our knowledge of the ventral surface is accordingly limited; articulated material of *Leiostegium* was described by Jell (1985), who concluded that a rostral plate was present. The likely conterminant hypostomal condition of leiostegiaceans is shown by the sharp termination of the glabella at the border, at which there are prominent pits to articulate with the anterior wings of the hypostome (text-fig. 17), and by the fact that where the anterior cephalic border becomes wider, as it does in *Palocorona* Shergold, 1975, backward-curving paradoublure lines are developed comparable with those on *Proceratopyge* (see Jago 1987) which are associated with increase in width of doublure medially in conterminant condition. Hence there is no evidence that Leiostegiacea belong to Ptychopariida (or Libristoma).



TEXT-FIG. 17. Leiostegiacea and possible relatives. *a*, cranidium of *Leiostegium*, early Ordovician, showing prominent anterior pits at border suggesting conterminant hypostomal attachment, $\times 3$; *b*, cranidium of late Cambrian *Peichiashania* (after Shergold 1980, pl. 27, fig. 1), $\times 2.5$; *c*, early Ordovician *Theamataspis* (Scutelluinae) (after Fortey 1980), $\times 5$. If preoccipital muscle impressions in *b* and *c* are homologous, this may provide evidence of leiostegiacean ancestry of Illaenacea via tsinaniids (see text).

It seems possible that the Leiostegiacea also belongs within the Corynexochid/Illaenacean group. Many leiostegiaceans show a corynexochoid glabellar form: *Leiostegium* (Jell 1985, pl. 22, fig. 11; Shergold 1975, pl. 45, fig. 7), *Pagodia* (*Oreadella*) (Shergold 1975, pl. 36, fig. 1) *Annamitella* (Fortey and Shergold 1984, pl. 34, figs. 1–5, 7) and *Parakoldinioidia* (see Taylor and Halley 1974) from various families. The last-named is a member of the family Missisquoiidae, which was assigned to the Leiostegiacea by Shergold (1980), but which has been claimed (Ludvigsen 1982) as lying at the 'root' of the post-Cambrian radiation of the styginids (a contrary view was expressed by Lane and Thomas 1983). Shergold (1975) assigned the effaced family Tsinaniidae to the Leiostegiacea; in the *Treatise* (Lochman-Balk in Moore 1959) this family was considered to belong to Asaphacea (and

hence to Libristoma). I think Shergold is correct in removing tsinaniids from Asaphacea. For all their general dorsal effacement, tsinaniids show prominent muscle impressions lying outside the axial furrow opposite the posterior part of the palpebral lobes. These are like the 'lunettes' of illaenids, and the homologous impression on styginids, and may be a synapomorphy. A similar impression exists on some more conventional leiostegiaceans, such as *Peichiashania* (Shergold 1980, pl. 27, fig. 1; see text-fig. 17 herein). These structures are distinctive enough to suggest they may be homologues. All the evidence combines to indicate that leiostegiaceans may be part of an enlarged illaenid/styginid/corynexochoid group.

3. *Superfamily Damesellacea*. The damesellaceans are regarded as the primitive sister group of the Odontopleurida, and should be placed in that Order. As in that group the hypostomal condition (see, for example, Chatterton and Perry 1983) was conterminant, and there is no evidence to suggest natant ancestry. Characters shared between odontopleurids and damesellaceans include: 1, narrow, (sag.) ledge-like anterior cranial border, which the glabella abuts sharply; 2, deeply scribed and inflated eye ridges; 3, transverse hypostome with relatively wide posterior border; 4, spinosity, especially pygidium and anterolateral margins of free cheeks (not the odontopleurid *Selenopeltis*); 5, occipital tubercle without thoracic homologues (where known, apparently of Fortey and Clarkson's 1976 type D); 6, third glabellar lobe reduced or absent. The autapomorphy of Odontopleuridae is the unique bi-spinose thoracic pleural tip, not present on Damesellacea (*vide* Lu *et al.* 1965, pl. 72, fig. 6). The apparent stratigraphic gap between Damesellacea (mid to late Cambrian) and Odontopleuridae (early Ordovician to Devonian) has now been bridged with the recognition by Bruton (1983) and Thomas and Holloway (1988) of *Acidaspides praecurrens* Lermontova, 1951, from the Upper Cambrian of Kazakhstan, as a true odontopleurid; the pygidium of this species (Thomas and Holloway 1988, pl. 16, fig. 352) shows more axial segments than Ordovician odontopleurids, but is identical to certain damesellaceans in this regard. Thomas and Holloway (1988) joined many previous authors since Swinnerton (1915) in regarding Odontopleurida and Lichida as together constituting a monophyletic group (as repeated on text-fig. 19). This is not the only possibility, because as many characters support the Styginidae as the sister group of Lichida. Further investigation of damesellids should cast light on this matter.

THE PROBLEM OF THE ORDER PHACOPIDA

The Order Phacopida Salter, 1864 is the largest group outside Libristoma, and may eventually prove to belong within it. In current usage it comprises the Suborders Cheirurina, Calymenina and Phacopina. The Cheirurina and Phacopina are accepted as monophyletic groups, and the Calymenina usually so, but there is no consensus about their mutual relationships. Both Henningsmoen (*in* Moore 1959) and Bergström (1973) indicated 'ptychopariid' origins for Phacopida. The diagnosis of Phacopida by Henningsmoen (*in* Moore 1959) includes no characters peculiar to the group. Eldredge (1977, fig. 8) claimed that Calymenina were unrelated to Phacopina and Cheirurina, and placed them instead as the sister group of 'some Ptychopariina'. This certainly brings the Calymenina within the remit of the 'ptychopariid problem'. The alliance of Calymenina with Phacopida and Cheirurina was based on the close resemblance between their protaspides (Whittington and Evitt *in* Whittington 1954; Whittington *in* Moore, 1959; Chatterton 1971), including the presence of three pairs of prominent marginal spines, of which only two are cephalic (the 'phacopoid protaspis'). Bergström (1973) placed all three suborders (demoted to superfamilies) in different orders: Odontopleurida (Cheiruracea), Phacopida (Phacopacea) and Ptychopariida (Calymenacea). Again, this shows how different are opinions about high level trilobite classification. But whatever classification is closest to the truth, Phacopida have to be discussed in relation to Libristoma.

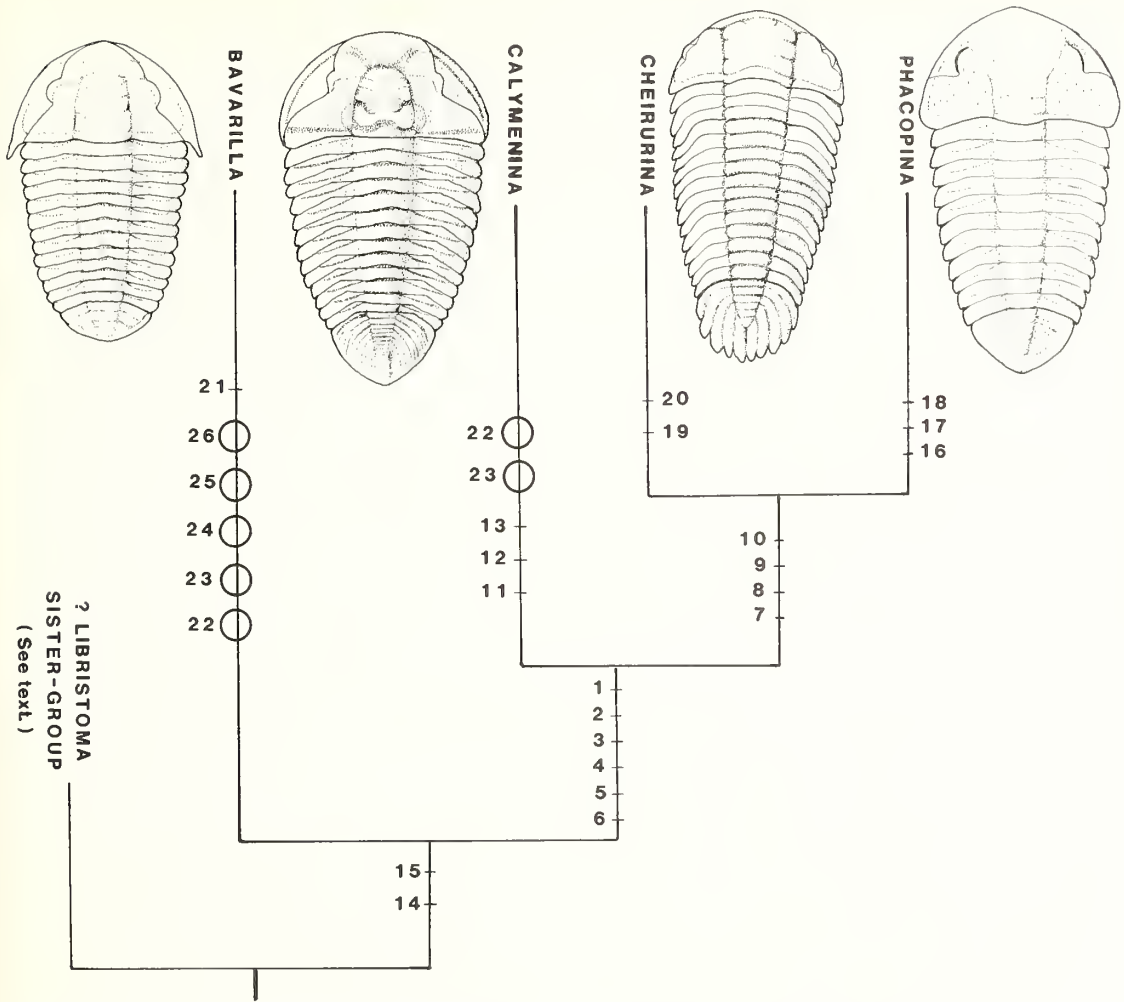
A list of possible synapomorphies can be cited as supporting the concept of Phacopida used in the *Treatise* (Henningsmoen *in* Moore 1959), shared between Calymenina, Cheirurina and Phacopina. These are:

1. The phacopoid protaspis type.
2. Loss of concentric terrace ridges on the cephalic doublure. As discussed above, cephalic doublural terrace ridges are primitive for the Trilobita and retained in Libristoma; their loss is significant.
3. Presence of hypostomal wing process. Although not widely figured this has been shown on representatives of all three groups by Whittington (1988b), and on an early cybeline by Fortey (1980).
4. Granulose surface sculpture. A characteristic densely granulose surface sculpture appears to be ubiquitous on early representatives of all three major groups (later Phacopina have much modified sculpture, but all stratigraphic evidence shows this to be secondary).
5. Absence of pygidial border in more primitive members of the group. Pleural and interpleural furrows usually extend very close to the margin and do not stop at a marginal upturned pygidial rim or flattened border so common in Libristoma. A 'pseudoborder' may appear on certain homalonotids such as *Plaesiacomia* (Henry 1980, pl. 23, fig. 4), but this is connected with coaptation, and is not homologous with borders of other trilobites.
6. Five or more pygidial segments. This number is known to be secondarily reduced in later Cheiruridae.

This list is sufficient to suggest that the *Treatise* (Moore 1959) Phacopida *does* constitute a natural group. I cannot find any of the alternative suggestions which have been made regarding ordinal relationships of Calymenina and Cheirurina supported by more characters which are likely to be synapomorphies. For example, of Bergström's (1973, p. 41) list of odontopleurid characters there are only two (nature of thoracic articulation and loss of cephalic doublure terrace ridges) which would support the inclusion of Cheiruracea in Odontopleurida.

If Phacopida includes Calymenina, Cheirurina, and Phacopina it is likely that the suborder Calymenina is the primitive sister group of Cheirurina + Phacopina, as shown by the distribution of characters summarized in text-fig. 18. Detailed discussion of these characters is beyond the scope of this paper, except to note that calymenaceans retain several primitive characters, such as the circum-ocular suture (uniquely among post-Cambrian trilobites) and tapering glabella. The question is whether any calymenines show evidence of having an ancestor with natant hypostomal condition, which would imply that they, like the Asaphida, should be included within Libristoma. All Phacopina and Cheirurina have attached, conterminant hypostomes, and we would expect natant ancestry to be revealed in the most primitive calymenaceans. *Neseuretus* is close to the common ancestor of Calymenidae and Homalonotidae, and, as noted above (text-fig. 3a), was conterminant. Probably still more primitive calymenaceans have clear preglabellar fields, and include *Prionocheilus* Rouault, 1847 (= *Pharostoma* of authors) and *Bavarilla* Barrande, 1868. Whittard (1960, pl. 18, fig. 4) illustrated a posterior extension of the doublure/rostral plate in *Prionocheilus* (after the manner of text-fig. 6), and in this form the hypostome was conterminant. So all Phacopida from the early Arenig onwards apparently have attached hypostomes, and the likelihood is that the relevant trilobites will be found in rocks of Tremadoc age or older. *Bavarilla* is Tremadocian, and was discussed in detail by Sdzuy, 1955. Most of its characters are primitive ones, even for libristomates: its hypostome is like that of generalized libristomates (Sdzuy 1955, pl. 6, fig. 50); it retains a pygidial border; it has a pygidium with only two (three?) segments; it does not show basal ('alar') muscle impressions in the cephalic axial furrows. In fact, its only likely phacopide character is the epifacetal type of pleural furrow (Sdzuy, pl. 6, fig. 55). Given that it also had narrow genal doublure (Sdzuy, pl. 6, fig. 52) and a preglabellar field it is not unreasonable to infer that the hypostomal condition was natant, unless the rostral plate were extended in the manner of *Prionocheilus*. So the position of *Bavarilla* as sister taxon of the Phacopida relies on a single character – and stratigraphical position, which may mislead. Since its hypostome is not known *in situ* its natant character is inferred, and on this alone would reside the placing of the Phacopida within the Subclass Libristoma.

I would be more enthusiastic about including Phacopida in Libristoma if some trilobites existed which had more of the phacopide synapomorphies whilst retaining the natant hypostomal condition. There are some late Cambrian trilobites which show other similarities to Calymenidae.



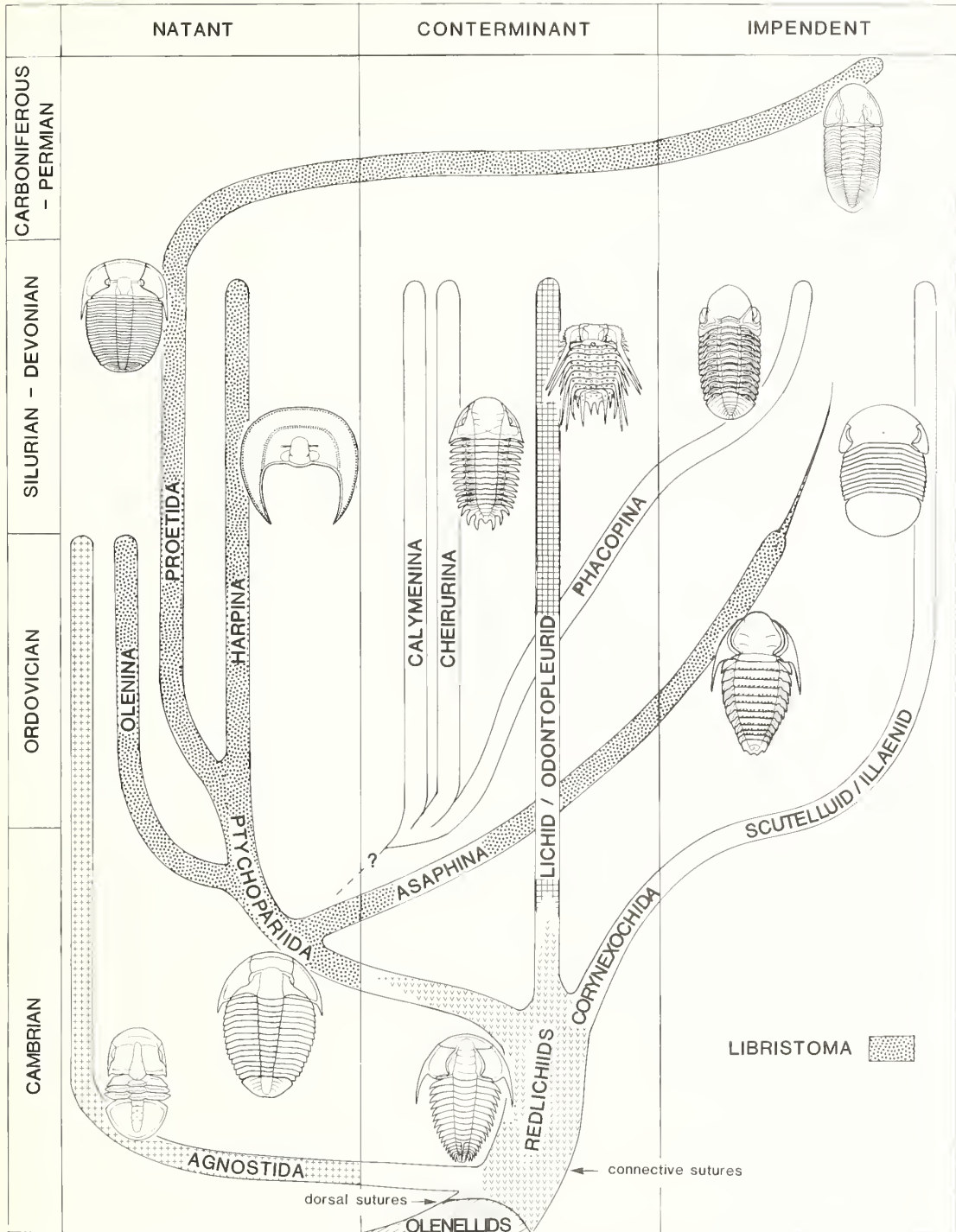
TEXT-FIG. 18. The most parsimonious cladogram of relationships of the main subgroups of Phacopina, emphasizing synapomorphies regarded as important, with *Bavarilla* as the sister group of higher Phacopida; retained plesiomorphic characters are shown as circles. Whether or not this group is a member of Libristoma depends on whether the sister taxon was natant (see text, p. 566). Primitive members of each group are illustrated: Calymenina, *Neseuretus*; Cheirurina, *Plimerops*; Phacopina, *Ormathops*. Characters: 1, phacopoid protaspis type (protaspis of *Bavarilla* is unknown and may prove of this type); 2, loss of concentric terrace ridges on cephalic doublure; 3, presence of hypostomal wing process; 4, densely granulose surface sculpture; 5, loss of pygidial border; 6, five or more pygidial segments (this character undergoes reversal in later Cheiruracea); 7, proparian suture; 8, forward-expanding glabella (there are a very few exceptions to this in Cheirurina + Phacopina); 9, loss of circum-ocular facial suture; 10, spongy-reticulate genal prosopon; 11, gonatoparian style sutures; 12, muscle pad in 'alar' position; 13, muscle pad at inner end of S1 (which may otherwise bifurcate); 14, loss of falcate pleural tips; 15, epifacetal pleural furrow; 16, schizochroal eye; 17, characteristic sigmoidal form of 3S; 18, loss of rostral plate by fusion of free cheeks (except the primitive phacopide *Gyrometopus* Jaanusson, 1975, which retains it); 19, spinose pygidial margin; 20, cheiruroid type of thoracic articulation (see Bergström 1973); 21, only two deep pygidial pleural, no interpleural furrows. Retained primitive characters: 22, circumocular sutures; 23, tapering glabella; 24, opisthoparian sutures; 25, generalized ptychoparioid glabellar furrows; 26, strong pygidial border.

Calymenidius Rasetti, 1944 has granulose surface sculpture, and similar glabellar structure to calymenids. There are no 'alar' muscle impressions on Cambrian *Calymenidius* spp., although they were present on an early middle Ordovician species described as aff. *Calymenidius* sp. ind. by Whittington (1965, pl. 59, figs. 10, 12–15), a species which might now be referred to *Protocalymene* Ross, a calymenid. *Cliffia* (see also *Kirengina* Ogienko, 1974) is worth mentioning because its pygidium (e.g. Westrop 1986, pl. 27, figs. 4, 6) is at least superficially like those of early calymenids and Phacopina, and the cranidium can be compared with that of *Neseuretus* in the anterior position of the eye, glabellar shape, and the like. It does not show any distinctive cephalic autapomorphy of Calymenina, and nothing is known of the hypostomal attachment. Search for Cambrian sister taxa of Phacopida may not be fruitless. In the meantime the evidence of *Bavarilla* and lonchocephalids such as *Calymenidius* is hardly enough to place Phacopida within Libristoma, to which it might well belong.

HISTORY OF HYPOSTOME ATTACHMENT

The history of hypostome attachment among the non-olenellid trilobites can now be summarized (text-fig. 19). It seems likely to be of considerable importance in understanding aspects of feeding and functional morphology bearing on the adaptive history of the group as a whole. Early Cambrian redlichiids had conterminant hypostomes. On other early Cambrian trilobites, like *Dolerolemus*, the preglabellar field became extended, the cranidial border was extended backwards as a plectrum, but the hypostome may have become detached from the doublure at later stages in the ontogeny. Redlichiid conterminant condition was retained and modified in paradoxidids, in which both the frontal lobe of the glabella, and the middle body of the hypostome became inflated. Spinose projections on the posterior margin of the hypostome, such as those on paradoxidids, are a common feature of trilobites with attached hypostomes throughout the Palaeozoic. If it is correct to identify the ancestry of corynexochid-styginid-illaenid and the odontopleurid-lichid groups within what would be currently classified as Redlichiida these groups originated in the Lower Cambrian and retained the primitive conterminant mode of hypostomal attachment until the very end of their history in the Devonian. By the mid Cambrian corynexochids included superficially asaphid-like trilobites (*Glossopleura*), and others that resembled Ordovician or later styginids, but in all of these rostral plate and hypostome were fused together.

The first Libristoma also appeared in the Lower Cambrian among the protolenids, trilobites which otherwise resemble contemporary redlichiids closely. The major 'radiation' of libristomates was in the middle part of the Cambrian, when highly effaced forms, or genera with eyes reduced or lost (polyphyletically), are found in different palaeoenvironments, sometimes to the exclusion of other trilobites. These libristomates may have been the first trilobites to exploit particle-feeding in deep sea environments. Libristomate hypostomes remained unspecialized for much of the Palaeozoic. One kind of conservative libristomate morphology persisted with little change from *Elrathia*-like forms in the mid Cambrian to *Aulacopleura*-like forms in the Devonian. Before the end of the Middle Cambrian the ventral median suture had developed in 'anomocaracean' asaphide libristomates, and the earliest secondarily conterminant hypostomal attachment appears in the asaphide group (*Proceratopyge*) shortly afterwards. In the Upper Cambrian these secondarily conterminant forms became important components of shelf faunas (Dikelocephalacea) but many different kinds of libristomates with unattached hypostomes persisted, notably Olenidae, which successfully occupied dysaerobic environments. Secondarily conterminant Asaphida started to develop modifications of the hypostome, such as wide borders, and posterior forks. It is interesting that the diversification of secondarily conterminant forms followed the eclipse of the primarily conterminant Corynexochida, some of whose morphologies they broadly reproduced. The Upper Cambrian record is overwhelmingly dominated by Libristoma, but if the relationships suggested in this paper are correct, primarily conterminant forms related to the lichid-odontopleurid and styginid-illaenid groups persisted through this interval. The Leiostegiacea and Damesellacea are regarded as primarily conterminant groups that bridge this 'gap'.



TEXT-FIG. 19. Simplified summary of history of hypostome attachment and the phylogeny of Trilobita, drawn as a tree. Secondary conterminant and impendent forms are derived from proetide sources after the disappearance of other conterminant clades. This may have happened first in the Silurian, but is not shown here for reasons of clarity.

By the early Ordovician natant hypostomes were confined to Proetida, and to a number of specialized groups persisting from the Cambrian (Trinucleacea, Harpina, Agnostina and Olenidae). Secondly conterminant asaphids and remopleurids were important and characteristic components of Ordovician faunas, but did not survive the Ordovician-Silurian boundary, at which level most of those natant families persisting from the Cambrian also became extinct (trinucleids, agnostids, olenids). At the same time the secondarily conterminant Asaphida also died out. Phacopida were important from the Ordovician onwards; all those we know had attached hypostomes, but the question of whether they had a natant, or primary conterminant ancestor is not satisfactorily resolved (see p. 565). The Odontopleuridae, Lichidae, Styginidae and Illaenidae with primary conterminant hypostomes diversified in the Ordovician and passed through to the Silurian and Devonian. Impendent hypostomal condition was common in the Ordovician (Cylopygacea, Illaenina, later remopleuridids) for the first time. Those groups with attached hypostomes developed hypostomal specializations in the Ordovician: forks, wide borders, enlarged maculae, varied surface sculpture. Natant hypostomes remained similar to those of the Cambrian.

From the Silurian onwards the natant condition persisted in Proetida alone, but within this group certain forms (*Warburgella*, *Cordania*) became secondarily conterminant. Again, one might speculate that these forms were filling niches unoccupied since the extinction of conterminant asaphids. In the Silurian impendent phacopids became widespread, and these continued into the Devonian.

After the end-Frasnian extinction of major trilobite groups, Proetida alone survived. Some of these were natant. But secondarily conterminant genera, such as *Paladin*, are also common trilobites in the Carboniferous – these developed hypostomal specializations like those of other conterminant trilobites. Certain phillipsiids (*Paraphillipsia*, *Cyphinioides*) became impendent, the first proetides to be so. I suspect that only secondarily conterminant and impendent hypostomal attachment persisted into the Permian, and the end of trilobite history (Owens 1983 has illustrated the relevant genera, none of which has a prelabellar field). So by the Carboniferous one group of Proetida were exhibiting the whole range of hypostomal attachment modes, although this group as a whole was primitively, and persistently, natant. As has been recognized for some time, some of these Carboniferous trilobites show parallelisms to earlier and unrelated groups – such as Phacopida. It does not seem likely to be coincidence that the proetids show such morphological novelty only after the demise of the conterminant groups (or impendent groups derived therefrom) which may have persisted all the way from the Lower Cambrian.

REMAINING PROBLEMS

Further problems in trilobite classification are legion. A number arise out of my analysis.

1. The relationships between the major subgroups of Libristoma, here treated as Orders and Suborders, are not resolved.

2. The relationships between the other high level taxa having primary conterminant hypostomal attachment are not resolved, neither between themselves, nor with the Libristoma. These appear merely as 'other trilobites' on text-fig. 14. These comprise, at the least: the Corynexochid/Illaenid/Leiestegiacean group; the Lichid/Odontopleurid group (if it is one); the Phacopida. Such evidence as there is, and it is feeble, places the last-named within Libristoma.

3. Redlichiida is only defined by not having one of the advanced characters of the other major trilobite groups with a rostral plate bounded by connective sutures. It is certainly a primitive group, and probably a paraphyletic group, which requires further analysis. Stability on the taxonomic status of higher level taxa cannot be achieved without resolution of some of these problems.

4. All these problems would benefit from phylogenetic analysis using one of the parsimony-based computer programmes for the production of dichotomous trees. The change from natant to secondarily conterminant is a major character reversal according to my treatment, and it would be interesting to see whether this was supported by other methods of analysis.

Acknowledgements. I cannot adequately express my indebtedness to the various colleagues and friends with whom I have discussed the ideas in this paper. Early drafts of all or part of the text were read by A. W. A. Rushton and R. M. Owens. Photographs were supplied by R. A. Robison, W. T. Chang and R. M. Owens; unpublished information was made available to me by H. B. Whittington, A. T. Thomas and M. D. Brasier. They do not share the responsibility for the ideas expressed herein, with which they may disagree, although all, I am sure, would sympathize with the problems that are raised. Claire Mellish drew text-fig. 19.

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Typescript received 6 April 1989

Revised typescript received 21 August 1989

BEDDING PLANE ASSEMBLAGES OF *PROMISSUM PULCHRUM*, A NEW GIANT ASHGILL CONODONT FROM THE TABLE MOUNTAIN GROUP, SOUTH AFRICA

by J. N. THERON, R. B. RICKARDS and R. J. ALDRIDGE

ABSTRACT. *Promissum pulchrum* Kovács-Endrödy, 1986, originally described as the earliest vascular land plant or an ancestor of the same, is shown to be a conodont. The species is represented by several spectacular bedding plane assemblages which occur in the Soom Shale Member of the Cedarberg Formation, Table Mountain Group, near Clanwilliam, South Africa. Invertebrate fossils from the Soom Shale indicate a late Ashgill (late Rawtheyan to Hirnantian) age. The conodont assemblages are the largest known, reaching 17 mm in length, with individual ramiform elements as long as 14 mm. The apparatuses are octomembrate with 2Pa, 2Pb, 2Pc, 2M, 1Sa, 4Sb, 2Sc and 2Sd elements. The possession of three pairs of P elements and a fully developed Sa-Sd symmetry transition series distinguishes *Promissum* from any other known conodont genus. The arrangement of the elements is unlike that shown by Carboniferous polygnathacean assemblages and implies a significantly different apparatus architecture. *Promissum* probably represents a cold-water Gondwanan lineage that survived the late Ordovician extinction event, and may well have given rise to the radiation of the Pterospirodontidae in the warmer Llandovery seas.

THE name *Promissum pulchrum* is unlike those commonly used for conodonts, and reflects the fact that Kovács-Endrödy (*in* Theron and Kovács-Endrödy 1986) originally described these fossils as the earliest known vascular land plants or their ancestors. The binomen means 'beautiful promise', an allusion to the perceived potential of the species in interpreting early land plant evolution. The interpretation of *Promissum* as a plant was not readily accepted by Rayner (1986), a referee of the paper, whose objections were published immediately following the Theron and Kovács-Endrödy (1986) preliminary report. These largely revolved around the lack of information normally required to substantiate a claim for vascular land plant status, principally the presence of tracheids, a cuticle with stomata, and sporangia containing trilete spores with sporopollenin-impregnated walls. Kovács-Endrödy (1986, p. 103) pointed out that her conclusions were based on comparative morphology and that no attempt had been made to obtain tracheids because the specimens were so few in number (twelve, including parts, counterparts and fragments). Scanning electron microscopy had revealed no preserved cell structure, but she took as important criteria the facts that the fossils were distinct, clearly outlined and typical of plants with hard cortical tissues, and that they had well developed spines.

It should be said that identification of these fossils is far from easy, and the attribution of them to the plant kingdom on grounds of general comparative morphology is not so surprising. Only after painstaking study did the present authors manage to establish them unequivocally as conodont apparatuses. The possibility was raised at one stage that they might be graptolites, again not an unreasonable suggestion as some do superficially resemble monograptids (see, for example, Theron and Kovács-Endrödy 1986, fig. 5). Rayner (1986) in his review of Kovács-Endrödy's conclusion referred to one of us (R.B.R.) as having decided that the fossils were *not* graptolites. The same comment is made by Kovács-Endrödy (1987) in her fuller description of *Promissum pulchrum*. These statements are not absolutely correct. R.B.R. examined only one specimen, figured by Kovács-Endrödy (1987) as pl. 3.5 (Pl. 3, fig. 2 herein): his service identification file records it as 'not a

graptolite...looks like a primitive jaw apparatus'. On publication of the Theron and Kovács-Endrődy (1986) paper, R.B.R. borrowed, through the kindness of the Geological Survey of South Africa and J.N.T., the remainder of the collection, quickly confirmed that none were graptolites, and rather more slowly concluded that they were conodonts. At this stage the help of R.J.A. was enlisted.

STRATIGRAPHY AND BIOSTRATIGRAPHY

In the rugged mountain ranges of the Southwestern Cape Province of South Africa a laterally persistent argillaceous unit, the Cedarberg Formation, forms a conspicuous and critical marker horizon (c. 120 m) among predominantly arenaceous rocks (3000 m) of the Table Mountain Group (text-fig. 1). The Table Mountain Group is the basal unit of the Cape Supergroup and rests unconformably on Precambrian metasediments and the Cape Granite Suite, which has been dated radiometrically at 500 to about 610 Ma (Burger and Coertze 1973; Schoch, Leygoine and Burger 1975). It is overlain conformably by the fossiliferous Emsian Bokkeveld Group.

The Cedarberg Formation thins northwards with concurrent thickening of the underlying glacial Pakhuis Formation, and is broadly divisible into two members: a lower Soom Shale Member and an upper Disa Siltstone Member (text-fig. 2). The dark grey, predominantly thinly laminated, micaceous Soom Shale Member seldom exceeds 15 m in thickness. It grades into or is intercalated with the underlying tillite of the Pakhuis Formation. Towards the north these basal units of the Cedarberg Formation in places display varvites/rhythmites and dropstones.

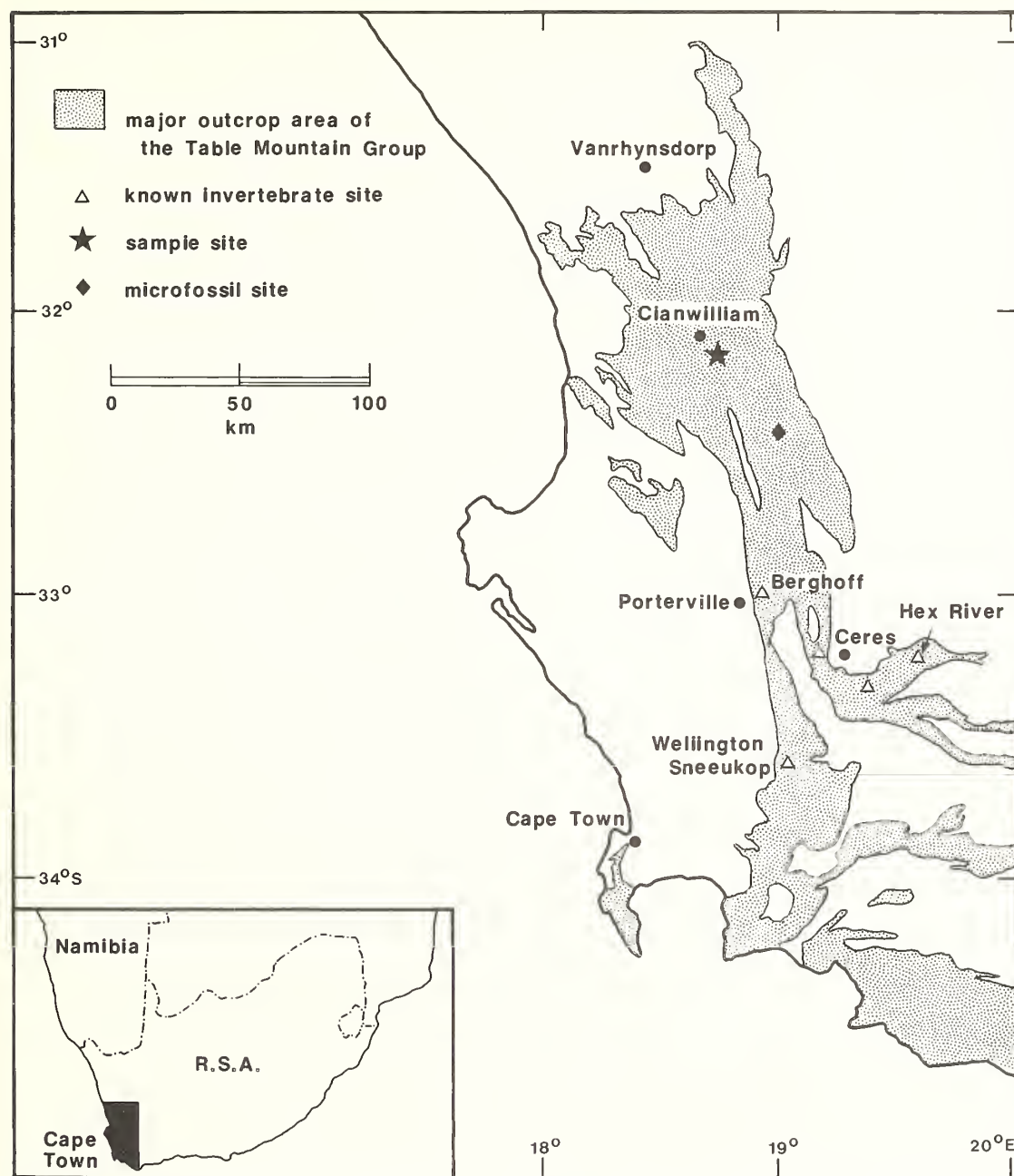
The Disa Siltstone Member is a thin-bedded argillaceous, fine-grained, sandy siltstone. Rare thin sandstone lenses become more prominent upwards, resulting in a gradational contact with the overlying Goudini Formation of the Nardouw Subgroup. Approximately in the middle of the Disa Siltstone Member in the Porterville-Wellington area occurs the 'brachiopod zone' in which Rust discovered a shelly fauna (Cocks *et al.* 1970; Cocks and Fortey 1986).

Body fossils from the Cedarberg Formation are as yet restricted to the western outcrops, and those on the farm Keurbos, about 11.5 km south-east of Clanwilliam, represent the northernmost fossiliferous occurrence known (text-fig. 3). The specimens of *Promissum* described in this paper all come from the base of the Soom Shale Member on Keurbos and were collected by J. N. Theron, J. H. Bredell and D. J. Barnardo of the Geological Survey in 1981. The associated fossils include rare scolecodonts, unidentified trace fossils, and a dark-coloured tube-like fossil which Kovács-Endrődy (1987) referred to the plant *Eohostimella* Schopf.

Quarrying for road metal has revealed that the Soom Shale locally attains a thickness of 6.5 m and contains a variety of invertebrate fossils. A 50 cm thick layer of partly bedded reworked glacial sediment interposes here between the underlying Pakhuis tillite and the shale unit. Systematic investigation of the quarry face has revealed two distinct levels at which *Promissum* and '*Eohostimella*' preferentially occur, 1.2 and 2.5 m above the Pakhuis/Soom contact. *Promissum* fragments are also present in the uppermost 5 cm of the reworked glacial bed, only 45 cm above the Pakhuis tillite. The Soom Shale Member at Keurbos is often conspicuously finely laminated with the individual laminae extensively characterized by linear and/or sinuous surface trails. *Promissum* and '*Eohostimella*' are infrequently present on the same laminar surface as brachiopods.

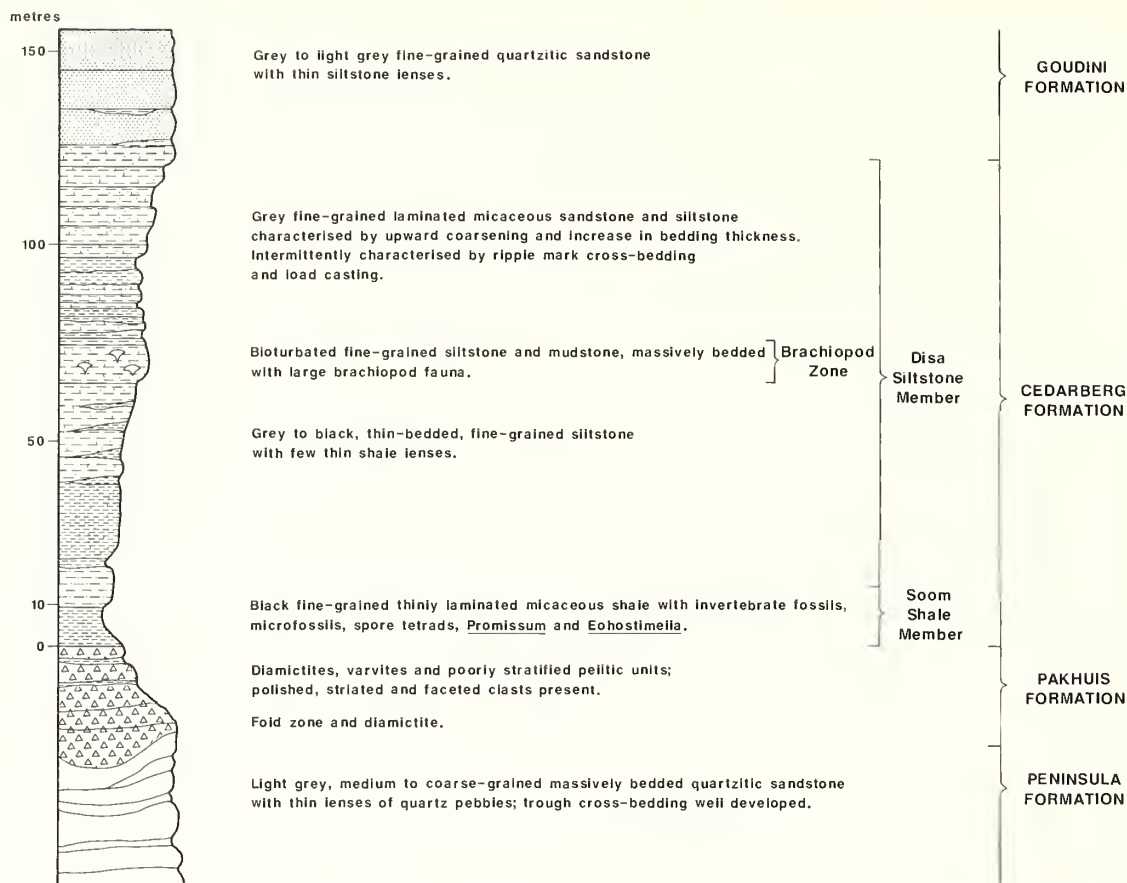
At least two major advances of the Gondwana ice sheet are registered in the glaciogenic deposits of the Pakhuis Formation (Rust 1967, 1981). The concurrent glacioeustatic fall in sea level resulted in partial reworking of glaciogenic deposits by coastal processes in a shallow marine embayment. The Cedarberg Formation was deposited during the succeeding glacioeustatic rise in sea level and represents the outwash silt and mud from the retreating ice sheets. Downwasting of the ice would have uncovered local embayments (ice-dammed?) along the northern shoreline which were probably flooded with fresh glacial melt-waters. The fine mud was clearly deposited towards the north in glaciolacustrine to shallow marine environments as shown by the presence of chitinozoans, marine phytoplankton, brachiopods, algae and spore tetrads in the same samples or in close proximity (Cramer *et al.* 1974; Gray *et al.* 1986). Varvites do not form in seawater (Flint 1971; Wright and Moseley 1975), but are commonly deposited seasonally in glacial lakes as graded layers. The finely laminated sediments at Keurbos with their biota of *Promissum*, '*Eohostimella*' and brachiopods manifestly accumulated in a protected still-water marine environment rather than in a proglacial lacustrine setting as previously envisaged (Theron and Kovács-Endrődy 1986).

Theron and Kovács-Endrődy (1986) regarded the basal Soom Shale Member at Keurbos as probably early Silurian (Llandovery) on the basis of spore tetrads, phytoplankton and chitinozoans (Gray *et al.* 1986). However, Cocks and Fortey (1986) demonstrated that the Soom Shale Member at Buffels Dome in the Hex



TEXT-FIG. 1. Locality map showing the distribution of the Table Mountain Group, the microfossil site reported by Gray *et al.* (1986) and the sample site for the specimens of *Promissum pulchrum*.

River Mountains is late Ashgill (late Rawtheyan to Hirnantian) in age. The crucial element in the fauna is the trilobite *Mucronaspis olini*, which on all known records is late Ashgill; none of the other elements of the fauna contradict this. Buffels Dome is more than 100 km from Keurbos and diachronism cannot yet be ruled out, but the same authors reviewed the evidence for the age of the overlying Disa Siltstone Member and concluded from the presence of brachiopods, including *Trematis taljaardi* Rowell, *Marklandella africana* Cocks and



TEXT FIG. 2. Schematic stratigraphic profile.

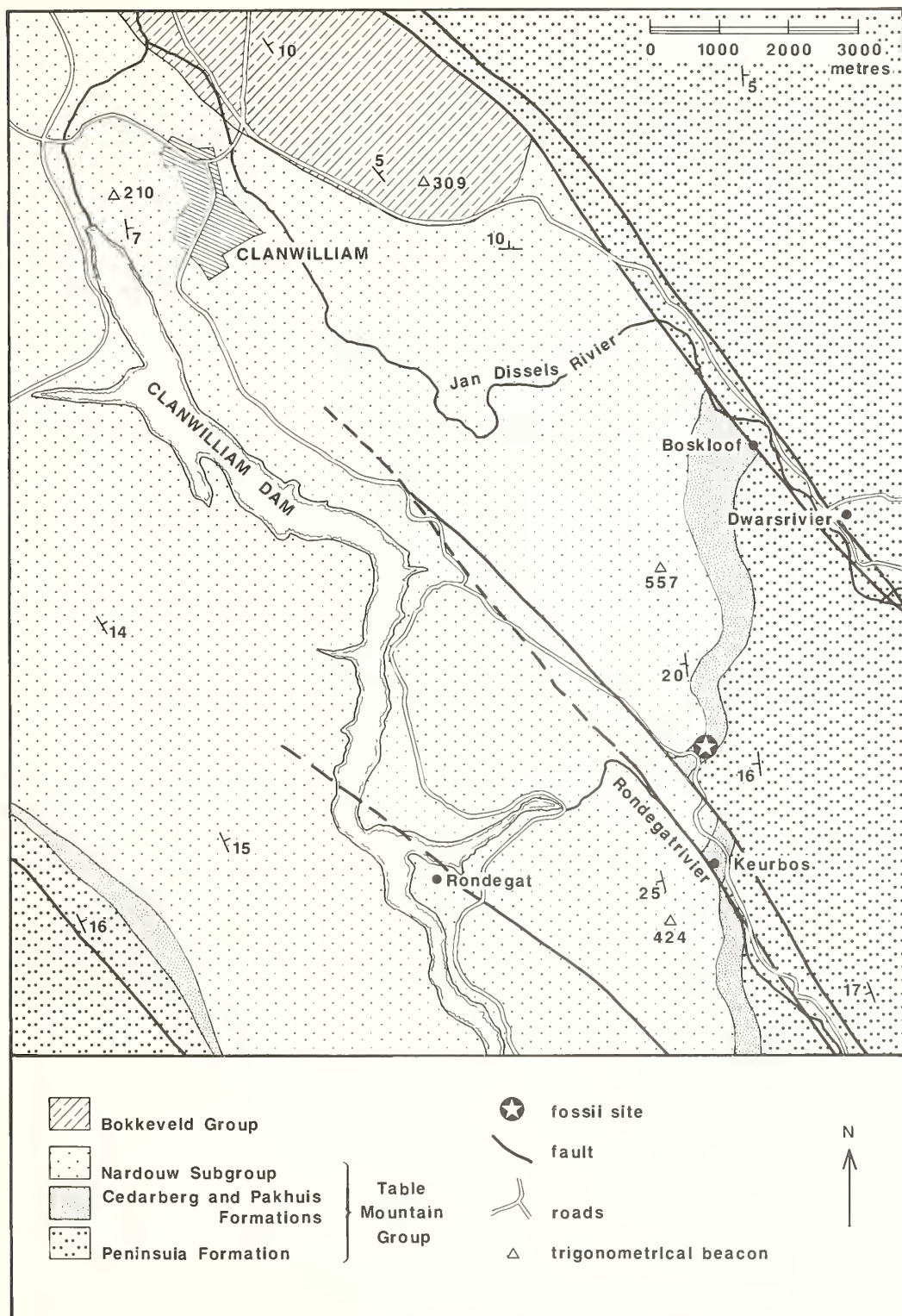
Brunton, *Eostropheodonta discumbata* Cocks and Brunton and *Plectothyrella haughtoni* Cocks and Brunton, that it is Hirnantian. Thus we regard *Promissum pulchrum* as more likely to be of late Rawtheyan to Hirnantian age, rather than Silurian.

PALAEONTOLOGY

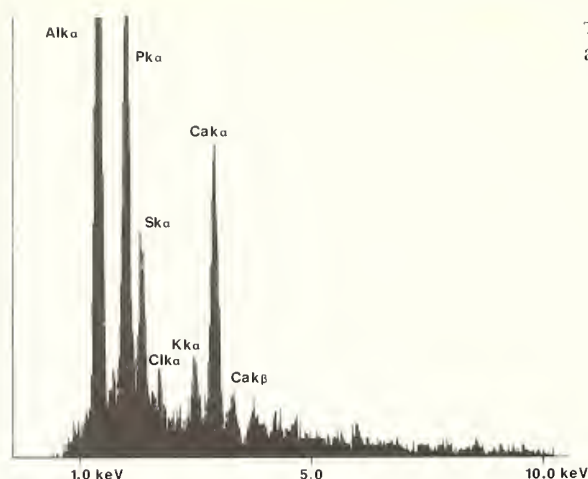
Introduction

Our examination of the specimens of *Promissum pulchrum* has shown that they are bedding-plane assemblages and isolated elements of conodonts. They are remarkable in several ways, not least in their spectacular size. The ramiform elements in the largest assemblage are more than 14 mm long, with the whole assemblage having a length of 17 mm. The elements are robust with peg-like denticles, between some of which finer denticles are apparent. Preservation of the original apatite is poor, with several of the elements represented only by internal and external moulds. In others the phosphate has been leached or replaced by clay minerals to give a pale greenish appearance. On analysis, this material gave peaks in aluminium, silicon and potassium. Peaks in calcium and phosphorus were obtained from some relatively unaltered amber-coloured areas of one of the ramiform elements (text-fig. 4).

The anterior and posterior ends of the assemblages can be determined from the anterior cusps and posterior processes of the ramiform elements. Beyond this, orientation is problematical, as almost all the elements have their 'upper' surfaces directed inwards and it is impossible to tell whether the

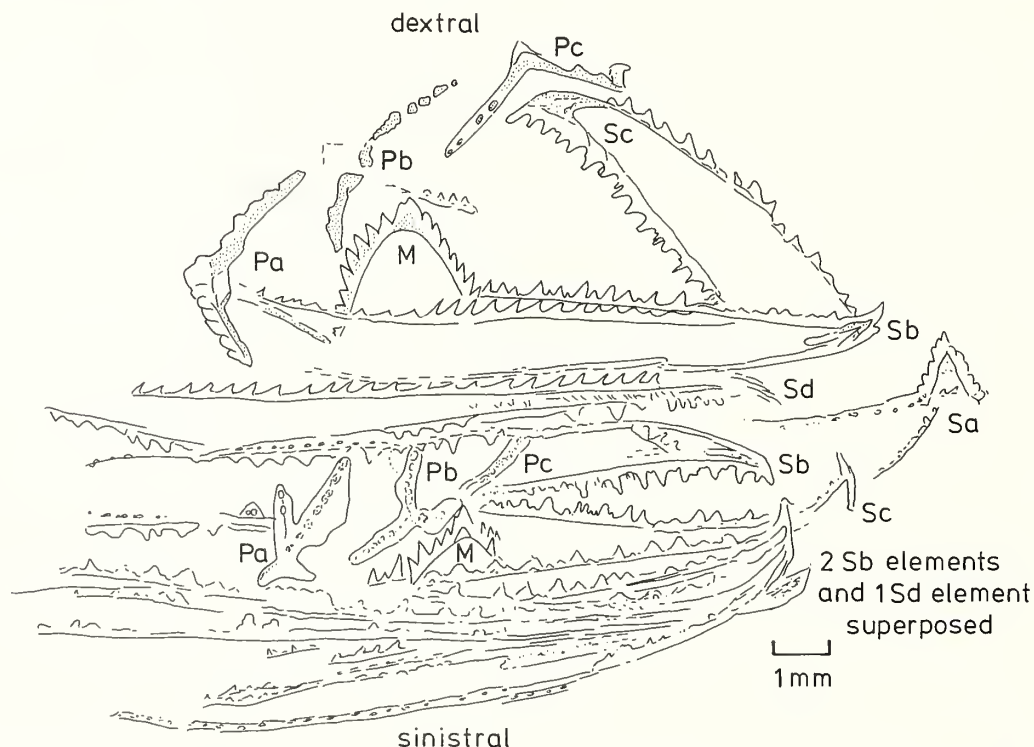


TEXT-FIG. 3. Geological map of the Clanwilliam area, showing the sample site.



TEXT-FIG. 4. Electron microprobe analysis of an amber-coloured area in a ramiform element of specimen C.1., showing principal excitation peaks.

assemblages are being viewed from above or below. The only guide is provided by the Pa and Pb elements in the central area of the holotype. On the counterpart (C.2b-I, text-fig. 5), these are preserved as deep external moulds, showing that their oral (conventionally 'upper') surfaces were directed into the bedding plane; they are thus being viewed from below, which indicates that they are situated on the sinistral side of the assemblage. This designation has been adopted in the description and discussion of specimens in this paper, but it should be emphasized that this is based



TEXT-FIG. 5. Camera lucida drawing of the counterpart of the holotype of *Promissum pulchrum*, specimen C.2b-I, for comparison with Pl. 1, fig. 2. The anterior of the apparatus is to the right.

on conventional orientation of the Pa and Pb elements alone and does not necessarily relate to actual left and right sides of the *Promissum* animal.

Systematic palaeontology

Genus *PROMISSUM* Kovács-Endrödy, 1986

Type species. *Promissum pulchrum* Kovács-Endrödy, 1986, from the basal Soom Shale Member, Cedarberg Formation, of Keurbos, near Clanwilliam, South Africa; by monotypy.

Diagnosis (emend.). Apparatus octomembrate, with 2Pa, 2Pb, 2Pc, 2M, 1Sa, 4Sb, 2Sc and 2Sd elements. Pa and Pb elements pastinate with deep basal cavities, M element arched, S elements with long processes.

Remarks. The apparatus is unlike that of any other known genus in possessing three pairs of P elements in conjunction with a fully developed Sa–Sd symmetry transition series.

Promissum pulchrum Kovács-Endrödy, 1986

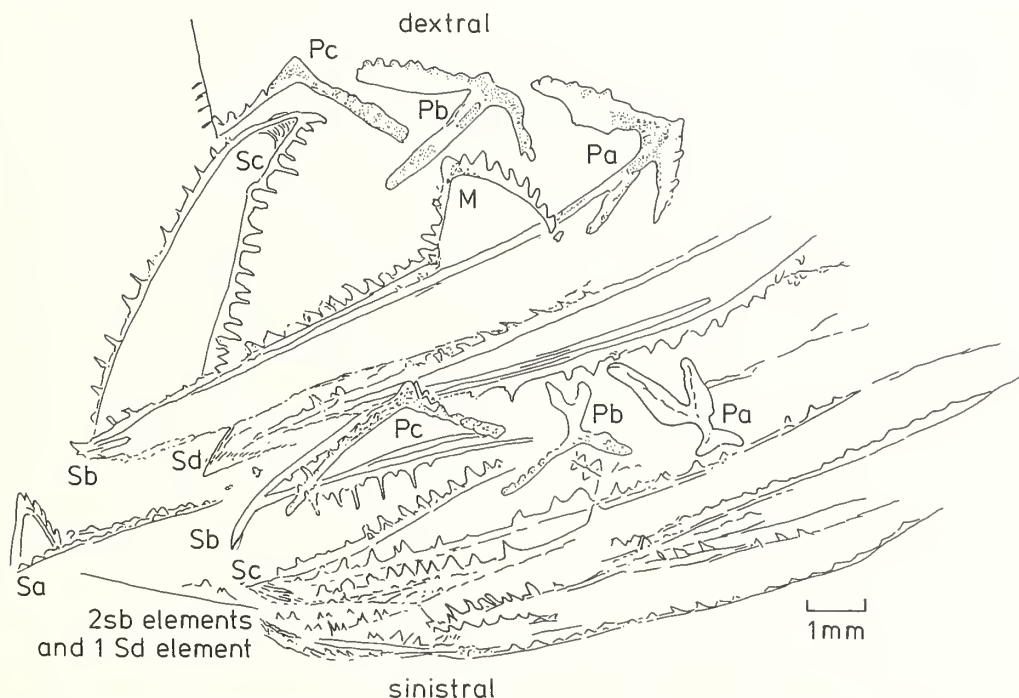
Plates 1–3; text-figs. 5–8

1986 *Promissum pulchrum* Kovács-Endrödy in Theron and Kovács-Endrödy, p. 102, figs. 4 and 5.

1987 *Promissum pulchrum* Kovács-Endrödy; Kovács-Endrödy, p. 99, pls. 3.1–3.22.

Holotype. Specimen C.2a, Geological Survey of South Africa, Pretoria.

Material. We have examined most of the specimens figured by Kovács-Endrödy (1987): the holotype C.2a (Pl. 2, text-fig. 6), its counterpart, C.2b-I (Pl. 1, fig. 2, text-figs. 5, 7, 8), assemblages C.1 (Pl. 3, figs. 1 and 4) and



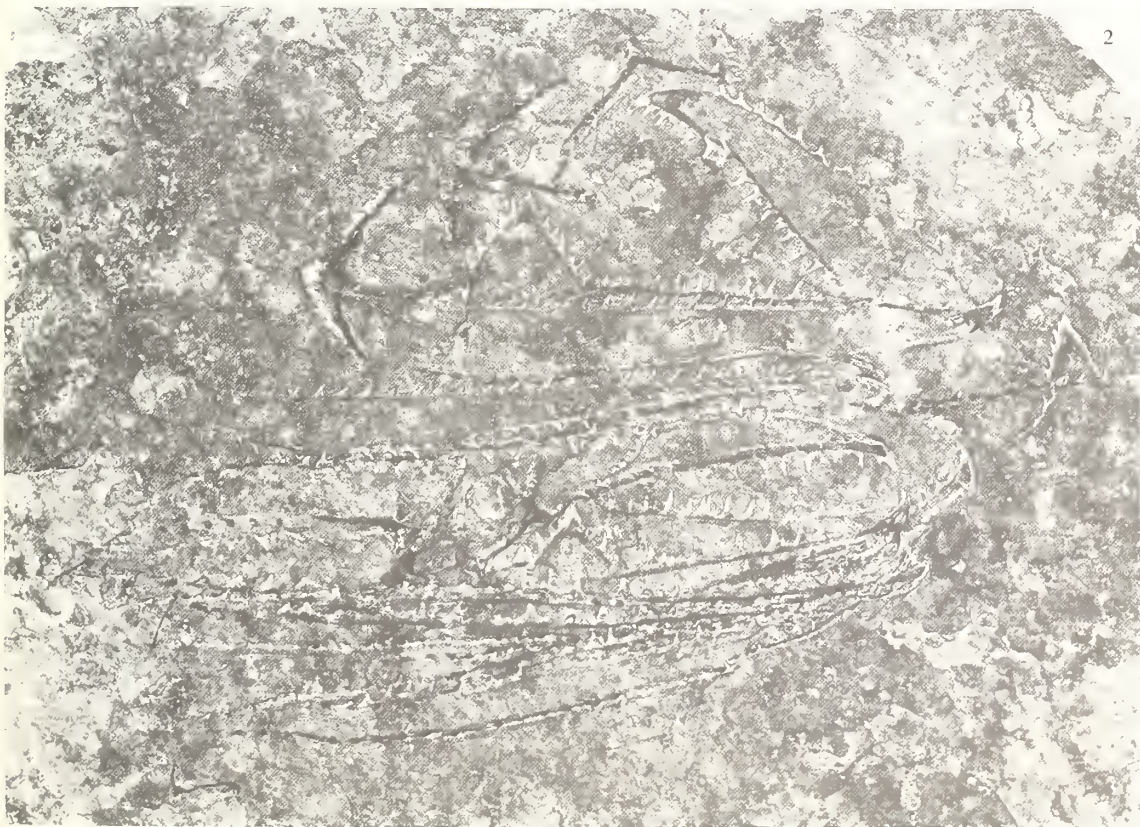
TEXT-FIG. 6. Camera lucida drawing of the part of the holotype of *Promissum pulchrum*, specimen C.2a. The anterior is to the left.



TEXT-FIG. 7. Scanning electron micrograph of latex cast of portion of counterpart of holotype, specimen C.2b-I, showing Pa element (above, centre), Pb element (below, centre) and portions of the processes of ramiform elements; posterior towards top, $\times 35$.

EXPLANATION OF PLATE I

Figs. 1 and 2. *Promissum pulchrum* Kovács-Endrödy. 1, latex cast of specimen C.2b-II. Anterior to the right, $\times 13.5$. 2, specimen C.2b-I, counterpart of holotype. Anterior to the right, $\times 7.5$. For annotation of the elements see text-fig. 5.



C.2b-II (Pl. 1, fig. 1), and isolated element C.6 (Pl. 3, fig. 2). The poorly preserved specimen numbered C.81 (Kovács-Endrödy 1987, pl. 3.6) and the unfigured specimen C.3 have not been included in our study.

Diagnosis. As for genus.

Description. Pa element: pastinate, high, with deep basal cavity; probably thin-walled. Cusp apical, stout; anterior, posterior and primary lateral processes with discrete nodose median denticles. Primary lateral process long, secondary lateral process short and apparently adenticulate.

Pb element: pastinate, high, with deep basal cavity; probably thin-walled. Anterior, posterior and primary lateral processes with discrete nodose median denticles. Primary lateral process long; distribution of secondary lateral processes unclear, but process disposition appears to differ from that shown by Pa element.

Pc element: indistinct, but with at least two denticulate processes diverging widely from a prominent triangular cusp.

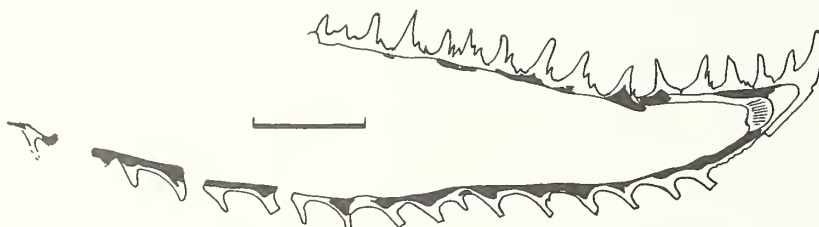
M element: symmetrically arched, with a prominent cusp and discrete, erect, robust denticles on each process. Basal cavity at apex of arch, with lip on outer side.

Sa element: alate, probably with long posterior process. Lateral processes diverge at 40–50° to form an anterior arch; very long, but broken about 1 mm from apex on all specimens, distal portions extend posteriorly for several millimetres. Proximal denticles stout, widely-spaced with u-shaped separations and no evidence of intercalatory smaller denticles; denticulation beyond 1 mm indistinct. Basal cavity apparently conical with small lips.

Sb element: tertiopodate, with very long posterior process bearing regular, stout, erect, large denticles between which smaller, slender denticles are irregularly recognizable. Antero-lateral process also long, curved proximally to become sub-parallel to posterior process, with widely-spaced, stout, conical denticles of subequal size. Outer lateral process not clearly preserved on any specimens, may be short and adenticulate or perhaps broken. Basal cavity small and conical beneath small erect cusp.

Sc element: bipennate, with very long posterior process displaying similar denticulation to that of the Sb element (text-fig. 8). Antero-lateral process strongly curved proximally to become nearly parallel to posterior process; very long and bearing widely-spaced conical denticles that are directed inwards and somewhat downwards. Basal cavity conical beneath a relatively small, erect cusp.

Sd element: quadriramate, with all four processes probably very long. Posterior process with similar denticulation to that of the Sb and Sc elements; other processes may have widely-spaced conical denticles, but they are difficult to distinguish. Cusp small and erect.



TEXT-FIG. 8. Camera lucida drawing of dextral Sc element of specimen C.2b-I, showing details of denticulation; scale bar 1 mm.

Remarks. Since Kovács-Endrödy (1987) considered *Promissum* to be a plant, she provided interpretations of various features of the specimens on that basis. These features are highlighted on the twenty-two illustrations of *Promissum* in her paper. Our recognition of the specimens as conodonts necessitates a re-interpretation, and we would caption her figures as follows:

EXPLANATION OF PLATE 2

Promissum pulchrum Kovács-Endrödy, specimen C.2a, holotype, photographed under alcohol. Anterior at the top, $\times 9$.



THERON, RICKARDS and ALDRIDGE, *Promissum*

- pl. 3.1 holotype of *P. pulchrum*, C.2a; complete octomembrate bedding-plane assemblage (see Pl. 2 herein).
- pl. 3.2 dextral portion of counterpart of holotype, C.2b-I; elements mostly preserved as external moulds. To the left are the P elements, the arrow points to the M element and the long processes of the S elements are evident in the centre and right of the picture. The displaced dextral Sc element is at top left.
- pl. 3.3 faintly preserved complete assemblage, C.2b-II; (a) cusps of ramiform S elements, (b) P element, (c) distal portion of S elements (see Pl. 1, fig. 1 herein).
- pl. 3.4 complete assemblage, C.1 (see Pl. 3, fig. 1 herein).
- pl. 3.5 isolated quadriramate Sd element, only proximal portion preserved (see Pl. 3, fig. 2 herein).
- pl. 3.6 poorly preserved processes of an S element.
- pl. 3.7 anterior portion of assemblage C.1, arched Sa element at the top of the picture (see Pl. 4 herein).
- pl. 3.8 cusps and proximal parts of two dextral S elements, C.2a.
- pl. 3.9 holotype, C.2a; (1) sinistral Pb element, (2) sinistral Pa element, (3) dextral Pa element, (4) dextral Pb element, (a) dextral Sb element, (b) axial portion of ramiform element group, (c) displaced dextral Sc element.
- pl. 3.10 dextral Pa element, C.2a.
- pl. 3.11 dextral Pb element, C.2a.
- pl. 3.12 portion of specimen C.2a, to show process disposition on Pa elements.
- pl. 3.13 sinistral Pa element, C.2a.
- pl. 3.14 Pa element, C.1.
- pl. 3.15 Pc element, C.1.
- pl. 3.16 central portion of complete assemblage, C.1.
- pl. 3.17 proximal portion of dextral Sb element, C.2a; the process on the right side of the photograph is part of the lateral process of the displaced dextral Sc element and shows robust denticles in lateral view.
- pl. 3.18 axial portion of the ramiform element group, showing opposition of denticulate surfaces, C.2a.
- pl. 3.19 proximal portion of dextral Sc element and dextral Pc element, C.2a.
- pl. 3.20 part of a process on the quadriramate Sd element C.6, showing robust denticles in apical view.
- pl. 3.21 enlargement of processes on S elements of C.1, showing robust denticles in apical view.
- pl. 3.22 cusp of dextral Sb element and portion of lateral process of displaced dextral Sc element, C.2b-I.

Arrangement of the assemblages and the architecture of the Promissum apparatus

The arrangement of the elements is most clearly displayed by the counterpart and part of the holotype (text-figs. 5 and 6), in which two integrated sets are evident:

(1) The elements of the first symmetry transition series (*sensu* Barnes *et al.* 1979). The Sb, Sc and Sd elements are orientated with their posterior processes parallel; other processes of these elements diverge at the cusp, but become parallel to the posterior processes distally. On the sinistral side of the assemblage these elements are piled on each other, with the cusps and denticulate surfaces of the posterior processes directed inwards. On the dextral side the elements are more widely separated. One of the dextral Sb elements and the probable Sd element are orientated in opposition to the sinistral elements, whereas the second Sb element has become overturned to face outwards. The dextral Sc element is also overturned and the proximal portion is displaced so that the long processes are directed inwards and somewhat anteriorly. The Sa element is positioned to the anterior of the other elements, displaced dextrally from the axis with the cusp pointing dextrally; the lateral processes are broken, with the distal portions parallel or subparallel to the processes of the other S elements.

(ii) the elements of the second transition series (*sensu* Barnes *et al.* 1979). The P elements are arranged in two parallel rows, aligned along an axis at 30° to that of the S elements. Those of the sinistral side are superposed on the processes of the S elements, but those on the dextral side are

EXPLANATION OF PLATE 3

Figs. 1 and 2. *Promissum pulchrum* Kovács-Endrödy. 1, specimen C1. Anterior at the top of the picture, $\times 9$. Specimens of '*Eohostimella*' are apparent around and across the apparatus. 2, specimen C.6. Single, isolated quadriramate Sd element. Anterior at the top, $\times 22$.



positioned largely outside the members of the first transition series. On the dextral side the Pa and Pb elements are in lateral aspect, whereas on the sinistral side of the part they are in upper view. The M element on each side is immediately to the left of its companion Pb element, with the cusp directed dextrally. As with the M elements, the Pc elements are in similar positions but apparently in opposing orientation on the two sides of the assemblage. The dextral Pc element on the counterpart has its denticulate posterior process directed away from the bedding surface while the equivalent process on the sinistral member is preserved as an external mould. The revealed face of the sinistral M element has a clear lip to the basal cavity that is not apparent on that of the dextral element.

The bilateral symmetry retained by the two sets of elements shows that the assemblage has been compacted in close to a dorso-ventral configuration. The displacement of the outer Sb and Sc elements on the dextral side, together with the apparent dextral shift of the axial Sa element, indicate that the apparatus was tilted a little to that side before it collapsed onto the bedding plane. This tilting has also displaced the P and M elements towards the right and may account for the different orientations of the Pa and Pb elements on the two sides.

The other two assemblages we have examined add little information about the relative dispositions of the elements in the apparatus. The second, less well preserved, assemblage (C.2b-II, Pl. 1, fig. 1) on the same slab as the counterpart of the holotype displays a similar arrangement of the two sets of elements, except that the upper surfaces of the Pa and Pb elements face inwards. The elements of the third assemblage (C.1, Pl. 3, fig. 1) are superposed on each other, giving a much more crowded arrangement in which the P and M elements cannot all be clearly distinguished; the anterior portion of the Sa element is separated from the others at the front of the apparatus in exactly the same manner as in the holotype (Pl. 4). The fact that all three specimens are preserved in close to dorso-ventral compaction may suggest that the *Promissum* animal was dorso-ventrally flattened in life, in contrast to the lateral flattening deduced for Carboniferous polygnathaceans (Aldridge *et al.* 1987).

In the absence of an assemblage compacted in lateral aspect, it is impossible to produce a reconstruction of the three-dimensional architecture of the *Promissum* apparatus. However, the evidence from these three specimens does place constraints on that architecture and reveals several important differences from the structure of polygnathacean apparatuses, as deduced from the study of several Carboniferous bedding-plane assemblages preserved in different orientations by Aldridge *et al.* (1987). In the polygnathaceans, the elongate, ramiform S elements were aligned at a steep angle to the long axis of the conodont animal, with their cusps to the anterior and an M element flanking them on each side; to the posterior of this group were one pair each of Pb and Pa elements, lying nearly vertically and nearly normal to the trunk. In *Promissum*, the M elements are clearly associated geometrically with the P elements, rather than with the S elements. In addition, unless the head of the *Promissum* animal has collapsed anteriorly on to the bedding-plane in all three known specimens, it appears that the P and M elements may not have been positioned posterior to the S elements in this apparatus. The superposition of the P and S elements suggests that the former were situated above or below the denticulate processes of the latter, although with the currently limited material it cannot be discounted that the two sets of elements may have been brought into juxtaposition by muscular contraction. Whether the cusps of the P elements were directed inwards or towards the S elements cannot be determined, but their position at least suggests that an analogy with the palatal tooth of the myxinoids is worthy of investigation.

EXPLANATION OF PLATE 4

Promissum pulchrum Kovács-Endrődy, specimen C1. Anterior area of apparatus, showing proximal portions of ramiform S elements. Anterior at the top, $\times 30$.

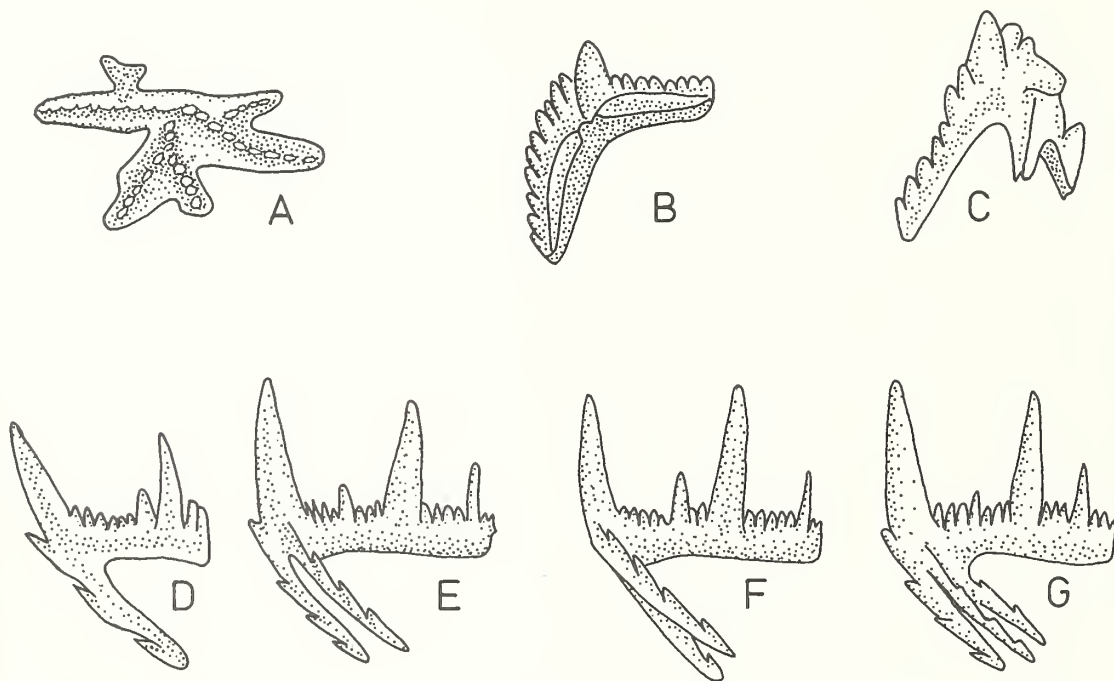


THERON, RICKARDS and ALDRIDGE, *Promissum*

RELATIONSHIPS OF *PROMISSUM* AND EVOLUTIONARY IMPLICATIONS

One of the striking features of *Promissum* is its extremely large size. Gigantism is not uncommon in cold-water taxa, although the controls in this case are uncertain. In other features, *Promissum* differs less spectacularly from other coeval conodont taxa. The apparatus structure broadly conforms to a prioniodontacean plan, although differing somewhat from all other genera whose apparatuses are known. The Sa–Sd elements compare in general pattern with those of the Ordovician genera *Prioniodus* Pander and *Amorphognathus* Branson and Mehl (Bergström 1971, 1983; see text-fig. 9), but the very long processes are distinctive. The M element is totally unlike that of *Prioniodus*, which is falodiform, or that of *Amorphognathus*, which is holodontiform. The Pa and Pb elements do resemble specimens that have been assigned to *Prioniodus*, but are most similar to the Pa element of *Sagittodontina* Knüpfer. The apparatus of *Sagittodontina* has been reconstructed by Bergström (1983), who included ramiform elements with very short processes, dissimilar from those displayed by the South African specimens. The material illustrated by Knüpfer (1967) from the same collections as the original specimens of *Sagittodontina* does include some broken specimens that may be comparable with some of the ramiform elements in *Promissum*, but nothing resembling the arched M element is reported. There have been no suggestions that *Sagittodontina*, *Prioniodus* or any other Ordovician genus possessed three pairs of P elements.

Some Silurian genera may well have had Pa, Pb and Pc elements homologous with those of *Promissum*. A quinquemembrate apparatus with three pairs of P elements has been reconstructed for *Pterospathodus* Walliser by Männik and Aldridge (1989), who also recognized Pa, Pb and Pc elements in their new genus, *Pranognathus*. Three P elements, termed Pa₁, Pa₂ and Pb were described in *Apsidognathus* Walliser by Uyeno and Barnes (1983), and comparable elements occur in



TEXT-FIG. 9. Element types in the apparatus of *Amorphognathus tvaerensis* Bergström for comparison with *Promissum pulchrum*; redrawn after Bergström (1983). A, Pa element, upper view; B, Pb element, lateral view; C, M element, lateral view; D, Sc element, lateral view; E, Sb element, lateral view; F, Sa element, lateral view; G, Sd element, lateral view.

Astropentagnathus Mostler. None of these genera have first transition series comparable with that of *Promissum* and quadrimate Sd elements, in particular, are unknown in Silurian taxa. Only in *Astropentagnathus* does the M element have a symmetrically arched morphology.

Pterospathodus, *Astropentagnathus* and *Apsidognathus* were all included by Klapper (1981) in the family Pterospathodontidae, which appears cryptically in the mid-Llandovery (Männik and Aldridge 1989). The earliest representatives are currently assigned to *Pranognathus*, which possesses thin-walled Pa, Pb and Pc elements, a dolabrate M element and a first transition series of Sa, Sb, Sc₁ and Sc₂ elements; related later Llandovery genera have more robust P elements, and in *Pterospathodus* the first transition series comprises only an Sa/Sb element. It is possible that *Promissum* represents a stock from which this group of genera descended by reduction of the first transition series. The radiation of the Pterospathodontidae may thereby reflect a spreading into warm Llandovery seas of a cold-water Gondwanan lineage that survived the late Ordovician extinction event.

Acknowledgements. This reappraisal of very exciting fossils would not have been possible without the very open and friendly cooperation of the original authors and the Geological Survey of South Africa. We especially wish to thank Dr C. MacRae for all his help. Dr A. Buckley carried out the probe analysis at Cambridge and Dr S. Conway Morris gave helpful advice on the fossils in the Soom Shale Member. Part of this work was funded by NERC Research Grant GR3/5105 to RJA.

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Typescript received 5 July 1989

Revised typescript received 7 December 1989

DRILLING AND PEELING OF TURRITELLINE GASTROPODS SINCE THE LATE CRETACEOUS

by WARREN D. ALLMON, JAMES C. NIEH *and* RICHARD D. NORRIS

ABSTRACT. Frequencies of predation on turritelline gastropods by drilling and peeling predators have not changed significantly during the course of the Cenozoic. Rates of drilling in the Cretaceous are lower than Cenozoic rates, but not significantly so. Conversely, rates of peeling and repair in the Late Cretaceous reach or exceed Cenozoic values.

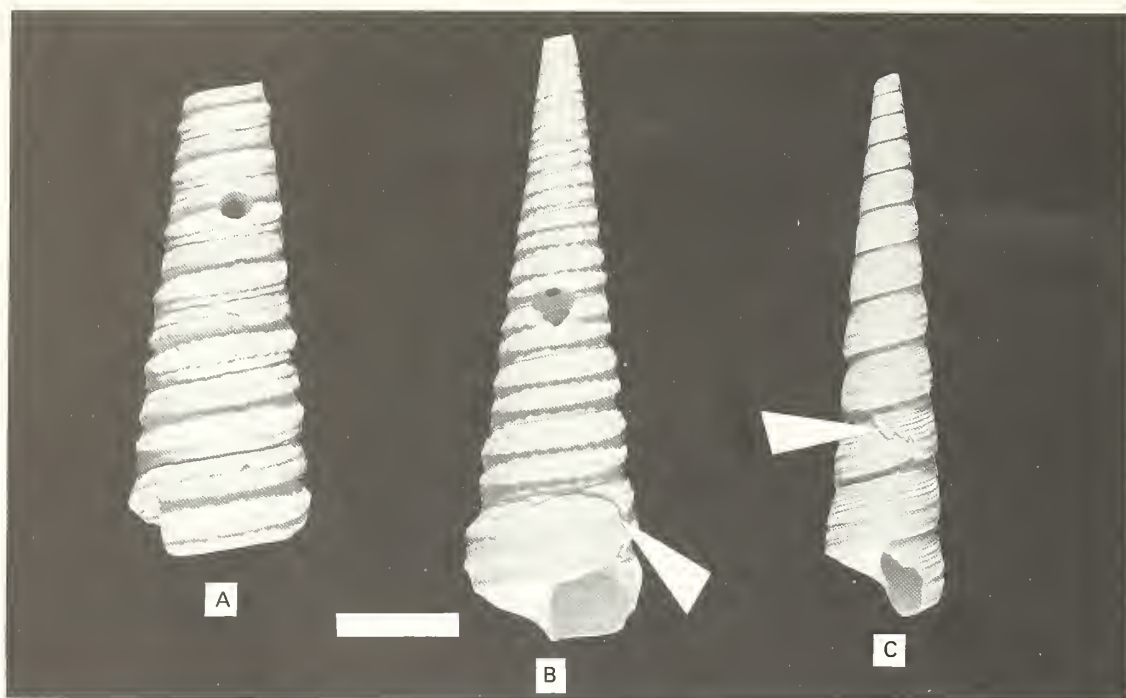
Turritelline shell form is not correlated with predation intensity. Highly sculptured species are not more immune to drilling and peeling predation than are less sculptured taxa. Shell geometry in these gastropods does not show progressive trends during the Cenozoic. Sculpture strength and most aspects of shell form and sculpture strength are evidently not adaptations to resisting peeling and drilling predation in turritellines. Turritellines have not evolved during the Cenozoic in an arms race to build more predation-resistant shells, although behavioural or other non-shell characteristics may have changed over time. Thus, in this group, any 'marine revolution' and adaptive response of prey to the evolution of durophagous predators must have occurred prior to the Late Cretaceous.

THE notion that predation influences the evolution of prey has been widely discussed (e.g. Vermeij 1977, 1978, 1982*b*, 1983, 1987; Hughes 1980; Bayne 1981; Kitchell *et al.* 1981; Bakker 1983; Taylor 1984) but has seldom been tested within a single prey clade. Turritelline gastropods (i.e. members of the family Turritellidae, subfamilies Turritellinae and Protominae, *sensu* Marwick [1957]) are common to abundant fossils in many Cretaceous and Cenozoic horizons, and many bear the marks of attack by drilling and shell-peeling (i.e. aperture-breaking) predators. Previous studies (e.g. Dudley and Vermeij 1978; Vermeij and Dudley 1982) have discussed trends in predation in this group, at least as represented by these traces. In this paper we expand this earlier work by (1) considering a much larger data set, (2) making use of more adequate views of both turritelline ecology (Allmon 1988*a*) and of the stratigraphic and systematic relationships of species from the southeastern United States (Toulmin 1977; Allmon 1988*b*), which have figured prominently in previous work, and (3) exploring possible evolutionary consequences of predation on turritelline shell form.

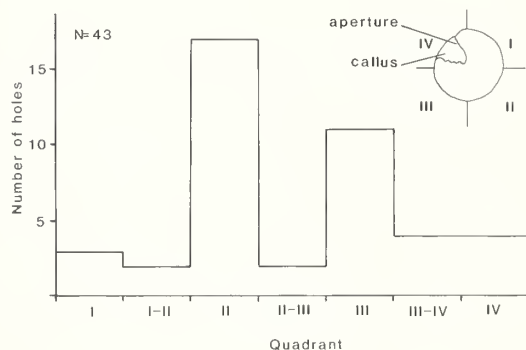
Vermeij (1987, and references therein) has long argued that durophagous predation has been at least partly responsible for some trends in gastropod shell morphology. Whether this has been the case for turritellines is of particular interest since almost nothing is known about the functional significance of most features of their shells. Correlation or lack of correlation between predation intensity and shell form over the history of this group may indicate evolutionary origins of particular features. Although their origin is obscure, turritellines appear to have arisen in the Late Jurassic or Early Cretaceous (Merriam 1941), a time of rapid morphological and taxonomic diversification among gastropods (Vermeij 1977; Taylor *et al.* 1980, 1983). An understanding of the factors controlling the occurrence and significance of predation in turritellines may thus also contribute to a better understanding of the evolutionary dynamics of this interval.

MATERIALS AND METHODS

New data presented here are derived from examination of specimens in the collection of the Department of Invertebrate Paleontology of the Museum of Comparative Zoology (MCZ), Harvard University. All are from



TEXT-FIG. 1. Traces of drilling and peeling predation in fossil turrillines. All specimens from the Pliocene Pinecrest Beds of southern Florida. A. *Turritella* cf. *T. apicalis* Heilprin, showing naticid drill hole in the middle of the whorl. B. *Turritella* cf. *T. apicalis* Heilprin, showing the less common positioning of a drill hole astride a suture between whorls. Peeling/repair scar indicated by arrow. C. *Turritella pontoni* Mansfield, showing peeling/repair scar, indicated by arrow. Scale bar = 1 cm.



TEXT-FIG. 2. Longitudinal distribution of drill holes on intact turrilline shells of all species in our data set (Appendix 1). Figure in upper right shows the base of a turrilline shell looking toward the apex parallel to the axis of coiling, indicating division into quadrants for recording the longitudinal position of drill holes. Intact bases and apertures are distinguished from broken and incomplete specimens by the presence of parietal callus on outside of last whorl.

Cenozoic deposits of the New World and most were personally collected by one of us (WDA). A total of 1097 specimens representing 27 species were examined. For each specimen the following observations or measurements were made: length (or estimated length if broken), maximum whorl diameter, presence/absence of drill holes (text-fig. 1A, B), hole diameter, position of the hole vertically on the whorl and relative to the aperture if this could be determined (text-fig. 2), diameter of drilled whorl, presence/absence and number of repaired shell breaks (text-fig. 1C), and diameter of broken-and-repaired whorl. All measurements were made with digital calipers to the nearest 0.1 mm. Frequency of drilling in each species is the number of drilled shells divided by the total number of shells of that species examined, expressed as a percentage. Frequency of peeling/repair is the total number of scars divided by the number of shells examined, expressed as a decimal

value. These data (Appendix 1), together with additional observations from the literature (Appendix 2) represent a total of 10,387 specimens of 68 species, ranging in age from Early Cretaceous to Recent.

As noted by Dudley and Vermeij (1978), the generic and subgeneric taxonomy of turritellines is unresolved, particularly for fossil species (Marwick 1957; Allmon 1988b). Consequently we refer all species to *Turritella sensu lato*. Despite this remaining uncertainty, however, it is reasonable to make use of recent and relatively uncontroversial opinions on the position of some taxa, and we have therefore excluded from consideration three Recent species included in the genus by Dudley and Vermeij (1978). '*T. erosa* Couthouy' and '*T. reticulata* Mighels' belong to the genus *Tachyrhynchus* Mörch (e.g. Abbott 1974), which Marwick (1957) places in the subfamily Pareorinae. '*T. duplicata* Linnaeus' is the type species for the genus *Zaria* Gray (Marwick 1957). We have also excluded fossil and living species assigned to the genus *Mesalia* Gray, including the Eocene species *M. regularis* Deshayes and *M. amekiensis* Eames, both of which were considered by Dudley and Vermeij. *Mesalia* and *Zaria* are placed in Pareorinae by Marwick. Whatever the generic placement of species within Turritellinae, these taxa are almost certainly only distantly related to the other species considered here.

In their study of turritelline specimens in the collection of the U.S. National Museum, Dudley and Vermeij (1978) assigned several strictly Palaeocene species (e.g. *T. mortoni*, *T. praecineta*) to the Eocene (see Toulmin [1977] and Allmon [1988b] for further discussion of stratigraphic relations of early Tertiary species). Reassignment of these species and examination of others provide the first estimates of drilling frequencies in turritellines from the Palaeocene of the southeastern U.S.

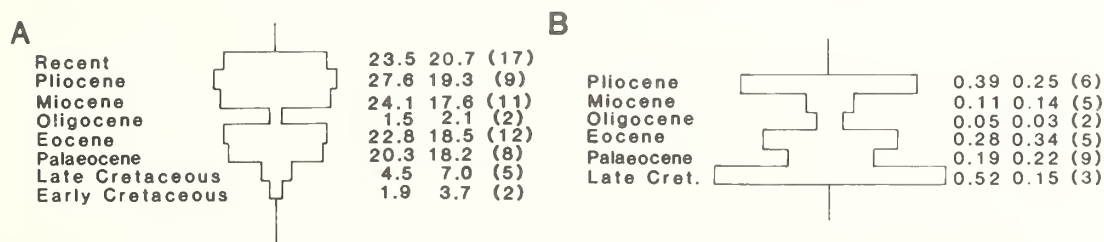
Drilled and undrilled shells may exhibit differential preservation potential (Dudley and Vermeij 1978; Taylor *et al.* 1983), but biases may operate in both directions. Drilled shells may be more easily fragmented or transported or, because many naticid predators pull their prey into the sediment to feed, they may increase the probability of preservation of drilled shells (Edwards 1974). Here we assume that all shells have equal preservation potential.

Most of the holes observed in these turritelline shells resemble the 'truncated spherical paraboloid' typically produced by naticacean gastropods (text-figs. 1A, B), rather than the usually more straight-sided holes characteristic of muricaceans (e.g. Sohl 1969; Carriker 1981). The great majority of holes examined here fall into types C, E and F of Arua and Hoque (1989), which these authors suggest as belonging to naticids. Specification of an exact percentage is difficult since many holes are eroded and cannot be assigned to one type over the other. Probably no more than 5–10% of the holes we examined are attributable to muricids, and we assume that the majority of drilling predators were naticids. We have also assumed that most of the observed breakage/repair scars were produced by shell-peeling predators, such as calappid crabs (cf. Vermeij 1982a, 1983), rather than accidental breakage not associated with predation (cf. Vermeij 1987, p. 227).

RESULTS

Temporal patterns

Early and Late Cretaceous drilling frequencies are not significantly different (*t*-test, $P = 0.32$), although both are well below almost all Cenozoic values (text-fig. 3A). Drilling frequency for all Cretaceous species taken together is significantly lower than that for Palaeocene, Miocene or Pliocene-Pleistocene species (Mann-Whitney *U*-tests, $0.025 > P < 0.05$), but not significantly different from



TEXT-FIG. 3. Distribution of rates of A, drilling, and B, peeling predation in turritelline gastropods in the Cretaceous and Cenozoic. First of three numbers on right is mean frequency (in % for drilling) of all samples for each time interval; second number is one standard deviation; third number is number of species sampled.

Figures derived from all data presented in Appendices 1 and 2.

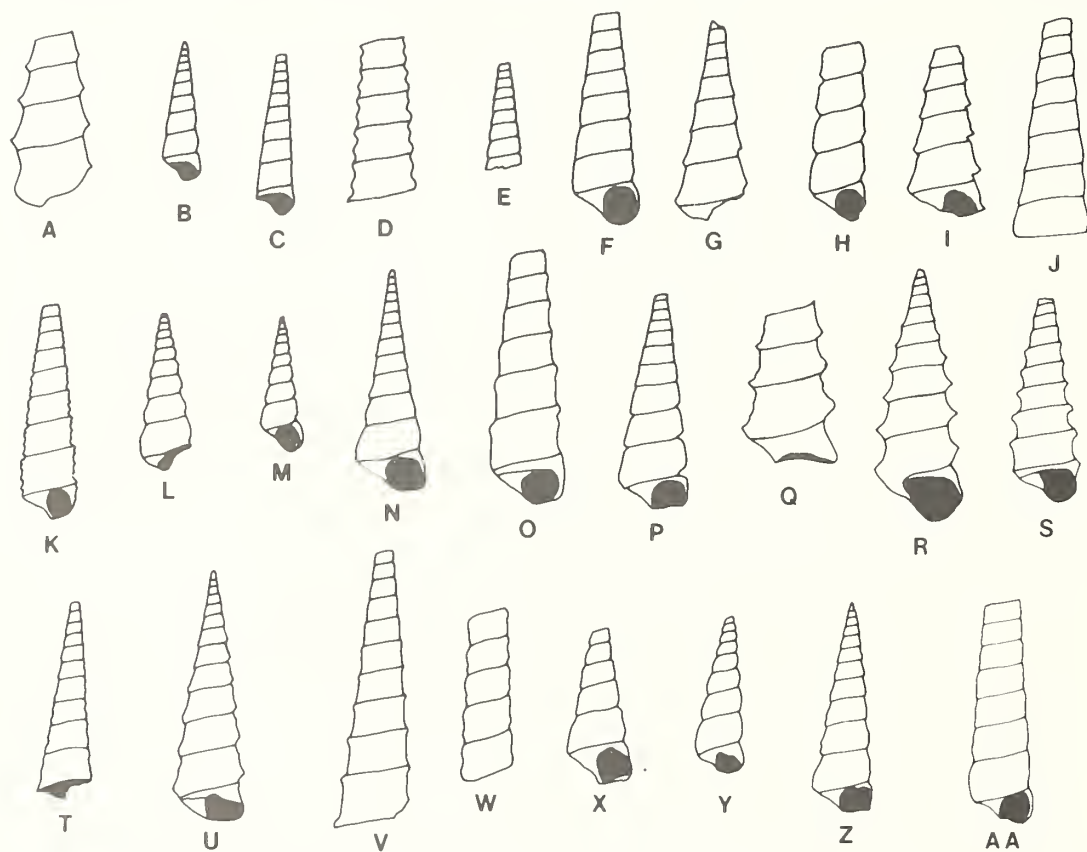
that for Eocene species ($P = 0.25$). Drilling frequency for the Oligocene is lower than that for either the Eocene or the Miocene (probably a result of small sample size), but the differences are not significant. In fact, no epoch of the Cenozoic shows a drilling frequency significantly different from any other (Mann-Whitney U -tests, $0.10 < P > 0.05$).

Late Cretaceous values for peeling/repair frequency, are higher, but not significantly so, than those of any epoch of the Cenozoic (text-fig. 3B). As is the case for drilling, peeling/repair values for each Cenozoic epoch are not significantly different from any other (Mann-Whitney U -tests, $0.10 > P > 0.05$).

Geographic patterns

Dudley and Vermeij (1978) stated that their data showed 'a distinct latitudinal trend in drilling predation for Recent species of *Turritella*', with tropical and subtropical shells showing drilling frequencies roughly three times those of temperate shells. Exclusion of the temperate *Tachyrhynchus* species from the group in our data set does not greatly alter this pattern. Of 212 shells collected above 30° latitude, 33 (15.6%) were drilled; of 766 shells collected below 30° , 226 (29.5%) were drilled.

Among fossil species only limited latitudinal comparisons are possible because of a paucity of

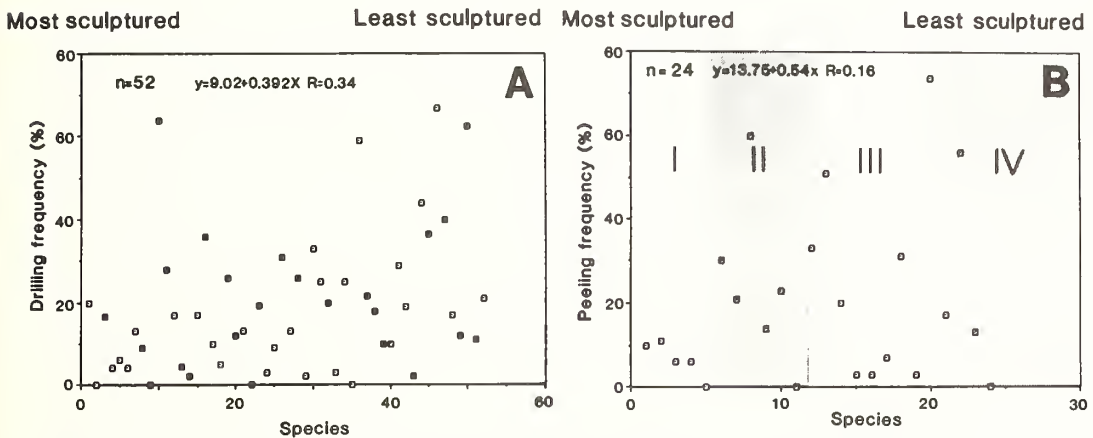


TEXT-FIG. 4. Whorl profiles of the 27 species examined in the present study (Appendix 1). A. *T. abrupta*, B. *T. alabamiensis*, C. *T. aldrichi*, D. *T. altilira*, E. *T. alveata*, F. *T. apicalis*, G. *T. carinata*, H. *T. cumberlandia*, I. *T. rina*, J. *T. rubicollis*, K. *T. eurynome*, L. *T. femina*, M. *T. gilberti*, N. *T. gladeensis*, O. *T. lunerosa*, P. *T. indenta*, Q. *T. larensis*, R. *T. postmortoni*, S. *T. praecincta*, T. *T. mississippiensis*, U. *T. mortoni*, V. *T. multilira*, W. *T. perattenuata*, X. *T. perdita*, Y. *T. plebeia*, Z. *T. pontoni*, AA. *T. wagneriana*.

approximately isochronous and geographically widespread samples. *Turritella mortoni*, *T. praecincta* and *T. humerosa* from the Palaeocene Aquia Formation of Maryland and Virginia lived at approximately the same time as *T. praecincta*, *T. postmortoni*, *T. multilira* and *T. eurynome* from the Palaeocene Tuscaloosa and Nanafalia Formations of Alabama (e.g. Hazel *et al.* 1984; Ward 1985). All of these species are relatively large forms with moderate to well-developed spiral sculpture (text-fig. 4). Of 137 shells of the four lower latitude Alabama species, 11 (8.0%) were drilled and the peeling/repair frequency was 0.299. Of 179 shells of the three higher latitude Aquia species, 33 (18.4%) were drilled and the peeling/repair frequency was 0.078. The single species in common to the two areas, *T. praecincta*, showed a lower frequency of drilling (17% vs. 38%) and higher frequency of peeling/repair (0.36 vs. 0.035) in Alabama than in Virginia.

Predation and shell form

When ranked on a subjective scale of strength of sculpture, highly and moderately sculptured species show relatively low frequencies of drilling (text-fig. 5A). Sculpture and drilling frequency are significantly negatively correlated (*t*-test, $0.025 > P < 0.05$). Despite this relationship, the nine most highly sculptured species as a group are not significantly less frequently drilled than all other species

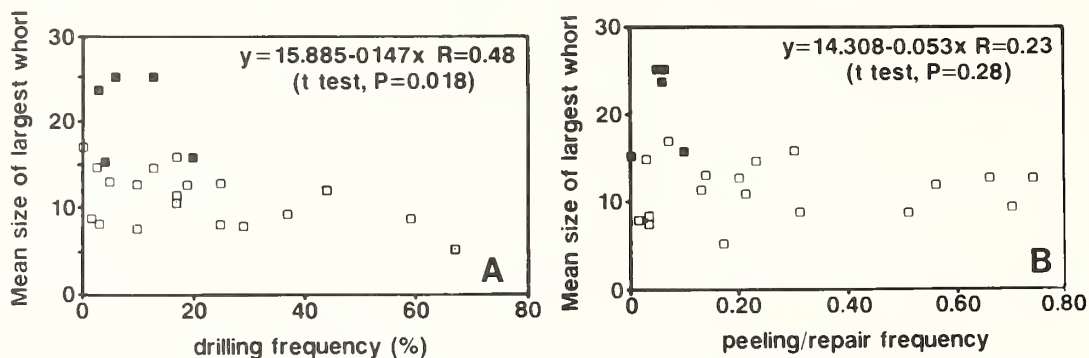


TEXT-FIG. 5. A. Drilling frequency vs. development of external spiral sculpture in 52 of the 67 turritelline species listed in Appendices 1 and 2. Species are arranged subjectively from least to most sculpture development along the horizontal axis as follows: 1. *T. praecincta*, 2. *T. postmortoni*, 3. *T. mauryana*, 4. *T. mortoni*, 5. *T. larensis*, 6. *T. abrupta*, 7. *T. rina*, 8. *T. berjadinensis*, 9. '*T. carinifera* Lamarck' (Recent, South Africa), 10. *T. gatunensis*, 11. *T. bicarinata*, 12. *T. altilira*, 13. *T. exoleta*, 14. *T. pagoda*, 15. *T. apicalis*, 16. *T. mariana*, 17. *T. eurynome*, 18. *T. multilira*, 19. *T. leucostoma*, 20. *T. variegata*, 21. *T. carinata*, 22. *T. trilira*, 23. *T. symmetrica*, 24. *T. femina*, 25. *T. vertebroides*, 26. *T. badensis*, 27. *T. cumberlandia*, 28. *T. nodulosa*, 29. *T. perattenuata*, 30. *T. pontoni*, 31. *T. gladeensis*, 32. *T. variabilis*, 33. *T. mississippiensis*, 34. *T. humerosa*, 35. *T. rubricollis*, 36. *T. aldrichi*, 37. *T. subangulata*, 38. *T. imbricatoria*, 39. *T. banksi*, 40. *T. alabamensis*, 41. *T. gilberti*, 42. *T. wagneriana*, 43. *T. howelli*, 44. *T. alveata*, 45. *T. bieniaszi*, 46. *T. indenta*, 47. *T. gonostoma*, 48. *T. perdita*, 49. *T. acropora*, 50. *T. annulata*, 51. *T. communis*, 52. *T. plebeia*. Open squares represent our observations (Appendix 1); solid squares represent previously published data (Appendix 2).

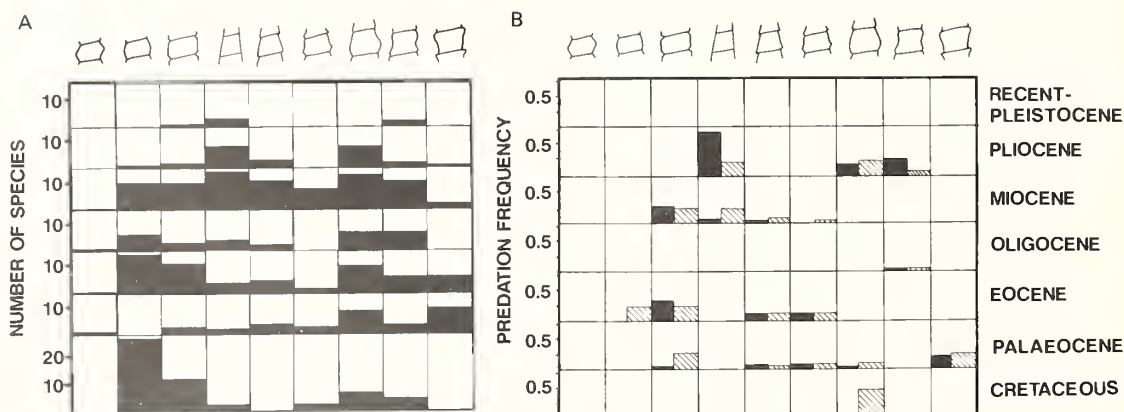
B. Peeling frequency vs. development of external spiral sculpture in the 27 turritelline species we have examined. Species are arranged subjectively along the horizontal axis, and numbered as follows: 1. *T. praecincta*, 2. *T. postmortoni*, 3. *T. mortoni*, 4. *T. abrupta*, 5. *T. larensis*, 6. *T. rina*, 7. *T. altilira*, 8. *T. apicalis*, 9. *T. eurynome*, 10. *T. multilira*, 11. *T. carinata*, 12. *T. femina*, 13. *T. cumberlandia*, 14. *T. perattenuata*, 15. *T. pontoni*, 16. *T. gladeensis*, 17. *T. mississippiensis*, 18. *T. humerosa*, 19. *T. rubricollis*, 20. *T. aldrichi*, 21. *T. alabamensis*, 22. *T. gilberti*, 23. *T. wagneriana*, 24. *T. alveata*, 25. *T. indenta*, 26. *T. perdita*, 27. *T. plebeia*. In an attempt to increase interpretability, groups of species indicated by Roman numerals were designated *a priori* on the basis of general similarity of degree of sculpture development; I = highly sculptured, II = moderately sculptured, III = weakly sculptured, IV = unsculptured.

together (Mann-Whitney U -test, $P = 0.48$). Similarly, the five most highly sculptured species as a group show lower peeling/repair frequency, although not significantly so (Mann-Whitney U -test, $P = 0.45$; text-fig. 5B). Peeling/repair frequency declines with increased sculpture, but not significantly so (t -test, $P = 0.135$). Frequencies of peeling/repair and drilling among less sculptured species range from very high to very low. (WDA and RDN independently arranged the 27 species in text-figure 5B according to their own judgments of 'strength of sculpture'; results for peeling/repair and drilling frequencies were essentially identical for both arrangements, suggesting confidence in the patterns despite subjectivity of the method.)

To assess the influence of spire height on peeling/repair frequency we computed length:width ratios for each shell and compared the distribution of peeled shells with the total sample. The two distributions are not significantly different (G -test, $P = 0.15$). Drilling frequency and peeling/repair frequency decline with increasing size of the largest whorl (text-fig. 6).



TEXT-FIG. 6. Mean size of largest whorl measured for each species plotted against frequency of A, drilling and B, peeling/repair. Size is negatively correlated with predation frequency in both cases, but not significantly so with peeling/repair. The five most strongly sculptured species are represented by solid squares. Elimination of these species does not change the correlation between size and drilling ($P = 0.027$), but does further reduce the significance between size and peeling/repair ($P = 0.48$).



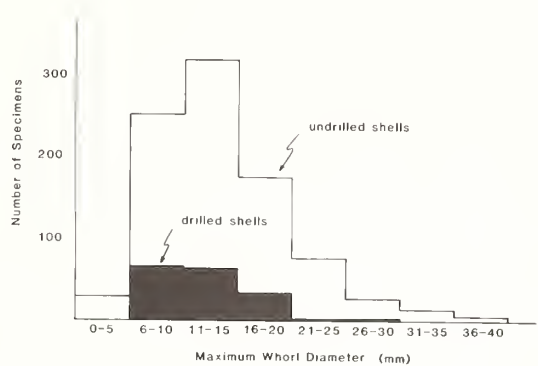
TEXT-FIG. 7. A. Classification of 197 Cenozoic and 43 Cretaceous turrnelline species from North, South and Central America and the Caribbean into nine whorl profile types proposed by Ida (1952) and used by Marwick (1971). This figure includes approximately 75% of the described species of *Turrnellia* from the New World. B. Predation frequencies (drilling in dark shading, peeling/repair in lighter shading) for turrnelline species according to whorl classification used in text-fig. 4. Text-figure based on only those species in common between the compilation used in text-fig. 4 and Appendices 1 and 2.

In turritellines, whorl profile can be examined separately from the external, mostly spiral sculpture (Marwick 1971; Allmon 1988*b*). In a sample of New World species, both the distribution of whorl profile types (text-fig. 7A) and the distribution of predation frequencies (text-fig. 7B), show little or no temporal pattern in drilling and peeling/repair data.

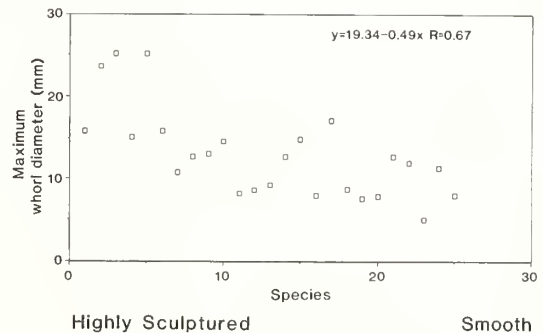
Size

Size distributions of drilled and undrilled shells in our data set are basically similar (text-fig. 8). For the 27 species we examined (although not for turritellines as a whole) size and sculpture development are significantly positively correlated (*t*-test, $P < 0.001$) (text-fig. 9).

TEXT-FIG. 8. Comparison of size distribution of drilled and undrilled shells in 1097 shells examined in the present study.



TEXT-FIG. 9. Plot of size (represented by maximum whorl diameter on Y axis) against the subjective ranking of sculpture development used in text-fig. 5B.

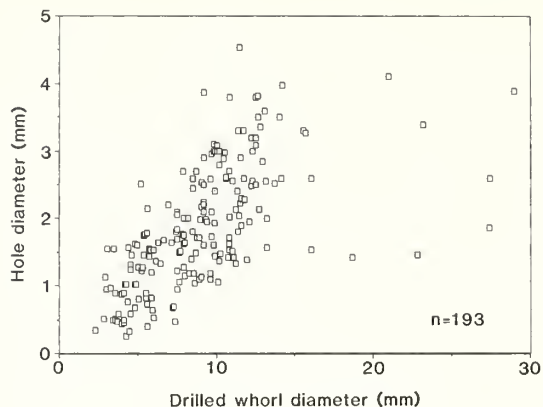


Incomplete drill holes

Only nine incomplete drill holes were observed in our sample: three each on specimens of *T. abrupta* and *T. eurynome*, and one each on specimens of *T. praecincta*, *T. larensis* and *T. humerosa*.

Predator and prey behaviour

Data on position of the drill hole relative to intact apertures indicate a high degree of selectivity on the part of the predators (text-fig. 2). Most holes are located on the half of the shell just behind the aperture (quadrants numbered II and III). This pattern is significantly different from the null hypothesis of a uniform distribution of holes around the circumference of the shell (*G*-test, $P < 0.01$). Drill holes vary in their vertical position on the whorl, but most (54%, $N = 170$) are located near the centre, rather than closer to either upper or lower sutures. Occasional holes are observed straddling a suture (text-fig. 1B). Diameter of the drill hole (a measure of predator size [e.g. Wiltse 1980]) plotted against maximum whorl diameter (a measure of prey size) shows that size of predator and prey are highly correlated (text-fig. 10).



TEXT-FIG. 10. Plot of drill hole diameter against diameter of drilled whorl.

DISCUSSION

Problems of pattern recognition

Studies of predation in the fossil record are potentially biased by a large number of factors. In any ecosystem, predation frequency on a given species will vary with abundance of predators, number of alternative prey, and the ranked preference relative to other prey. Only some of these factors can be assessed in the fossil record (e.g. Stanton and Nelson 1980; Stanton *et al.* 1981); for those that can be studied (e.g. abundance of naticids vs. potential prey species), few data are so far available from the coastal plain.

Preservable traces of predation may represent only a small fraction of actual predation on preservable prey species (Signor 1985; Vermeij 1987). Ansell and Morton (1987) have shown, for example, that some bivalves may be suffocated by naticid predators, leaving an incomplete borehole or no trace at all. Naticids are also known to attack gastropods through the aperture (Edwards 1969; Hughes 1985). Bottom-feeding fishes and asteroid echinoderms may be locally important predators of Recent turritellines (Allmon 1988a, and references therein), and will leave little or no record of such behaviour in the fossil record.

Interpreting possible evolutionary consequences of predation can be complicated in turritellines by the potential importance of non-shell characters in resisting predation. These include: (1) deep withdrawal into the high-spined shell (Vermeij *et al.* 1980; Vermeij 1982b, p. 708; 1987, pp. 195ff.; Allmon 1988a), (2) active escape by burrowing or crawling (Allmon 1988a), (3) seeking shelter among rocks (e.g. *T. banksi* – Dudley and Vermeij 1978) or in sponges (e.g. '*T. carinifera* Lamarck' – Kilburn and Rippey 1982), and (4) predator avoidance by small, patchily distributed populations or predator saturation by very large populations (Allmon 1988a).

Sample size must also be considered. Although our total data set is large, the sample of Oligocene and Cretaceous species is small. Both of these time periods are characterized by the lowest drilling frequencies we observe. Clearly one must wonder if these periods of reduced drilling intensity are real or are sampling artefacts.

Some or all of these factors may be responsible for the high variability in most of our results. Variability occurs within single species from the same area (e.g. *T. plebeia* from the Miocene of Maryland and Virginia, which shows drilling frequencies of 0–30%), within single species from different areas (e.g. *T. badensis* is 17% drilled in a Polish sample and 40.4% in a Bulgarian sample), among species within single time periods (e.g. high standard deviations in text-fig. 3), and among species within the group as a whole (text-fig. 5). Substantial variability also exists between species occurring in the same formation, and even the same outcrop.

Traces of drilling and peeling can represent two different phenomena (Vermeij 1982b, 1987). Frequency of incomplete drill holes (on shells without complete holes; see Kitchell *et al.* 1986; Vermeij *et al.* 1989) and frequency of peeling/repair represent frequency of unsuccessful predation.

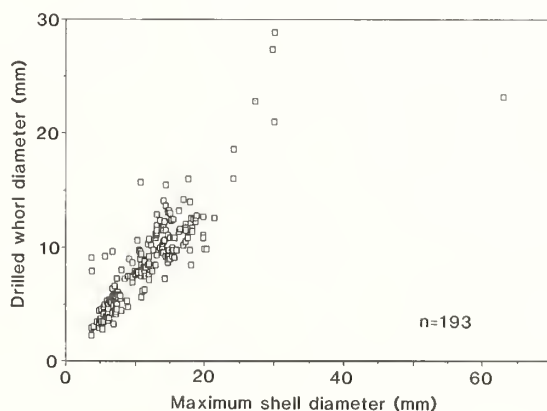
On the other hand, frequency of complete drill holes represents the frequency of successful predation. High frequency of unsuccessful predation indicates that predators are exerting strong selection pressure on prey, and that prey are successfully resisting most attacks (Vermeij 1982*a, b*). Low frequency of unsuccessful predation indicates either that few prey are being attacked (either because there are few predators or because by hiding or escape the prey avoid even the initiation of attack), or that most attacks are lethal. Low frequency of successful predation could indicate either that predators are rare or that prey avoid detection and capture. It is important to add that high frequency of successful predation may be evidence of intense demographic pressure (high predation-induced mortality) on a prey population, but not necessarily intense selective pressure for antipredatory adaptations (Vermeij 1982*b*).

Predator and prey behaviour

Although much is known about how naticids attack other molluscs (e.g. Ziegelmeier 1954; Sorensen *et al.* 1955; Fretter and Graham 1962; Gonor 1965; Edwards 1969; Taylor 1970; Berry 1982; Hughes 1985) naticid predation behaviour on turritellines is unknown. Observations of living turritellines (Allmon 1988*a*) show that the half of the shell comprising the two most-drilled quadrants in this study (II and III, text-fig. 2) is normally uppermost when the animal is actively crawling (aperture parallel to the substrate); quadrants I and II are normally uppermost when the animal is in a sedentary feeding position (aperture perpendicular to the substrate). Studies with living naticids and turritellines are required to determine whether naticids prefer the dorsal side of the turritelline shell, and actively manipulate them to this end, or whether the dorsal side is drilled because turritellines are frequently active crawlers.

The vertical distribution of holes over the whorls suggests that predators actively select the thinnest part of the shell for drilling. The correlation between size of drilled whorl and maximum whorl size of the drilled shell (text-fig. 11) suggests that for prey of any size, drilling predators tended to choose a whorl that was in the same relative position, usually two to three whorls behind the aperture (text-fig. 1*A*).

TEXT-FIG. 11. Plot of diameter of drilled whorl against maximum shell diameter of the drilled shell.



Geographic patterns

Geographic patterns in predation are more difficult to study in the fossil record than in Recent assemblages (e.g. Dudley and Vermeij 1978; Vermeij *et al.* 1989). In the case of the Palaeocene species from Virginia and Alabama discussed above, the situation is exactly the reverse from that seen among living species, with lower latitude species showing lower rates of drilling. Other factors may be involved in this case, including a relatively small latitudinal difference between the two areas ($< 10^\circ$), a weaker latitudinal temperature (and predation?) gradient during the early Tertiary compared to today (cf. Vermeij *et al.* 1980), and the small number of species considered.

Evolutionary significance

The idea that predation intensity in some way affects gastropod shell morphology has been considered by many authors (e.g. Vermeij 1978, 1982a, c, 1987; Raffaelli 1978; Hughes and Elnor 1979; Palmer 1979; Hughes 1980; Bertness and Cunningham 1981; Johannesson 1986; Thomas and Himmelman 1988), but we know little about the actual involvement of predation in the morphological evolution of a single prey clade. In the case of turritellines, Dudley and Vermeij (1978) have suggested that extreme development of carinae in *T. postmortoni* and *T. praecincta* from the Palaeocene of Alabama conferred protection from predation, since these species showed low drilling frequencies in their data. Our results show that well-developed sculpture confers only slight, if any, protection from either drilling or peeling attacks. While a significant negative relationship exists between sculpture and drilling frequency overall (text-fig. 5A), the most highly sculptured species are not significantly less drilled as a group than are less sculptured species as a group. Furthermore, the weak relationship that is observed between sculpture and drilling intensity can be explained as an effect of prey size.

The most sculptured species are larger than less sculptured species (text-fig. 9). The larger size of strongly sculptured taxa contributes to their lower frequencies of drilling and peeling (text-fig. 6). Since large size is correlated with reduced predation intensity, any correlations between sculpture development and predation are confounded by size effects (A. R. Palmer, pers. comm.). The size effect, however, should strengthen the correlation between highly sculptured, large species and low levels of predation. In fact, this correlation is quite poor, and shows that despite the help size effects proved to boost the fit, sculpture development is very poorly related to predation frequency.

Anecdotal indications of a relationship between sculpture and predation come from examination of co-occurring species. *T. mortoni* and *T. humerosa*, for example, occur in the Upper Palaeocene Aquia Formation of Maryland and Virginia. *T. mortoni* has more pronounced sculpture, consisting of several carinae, the largest of which is very strong and occurs near the base of the whorl. *T. humerosa* has fainter sculpture, consisting of fine spiral lines over the entire whorl and a pronounced but rounded subsutural collar. *T. humerosa* shows a drilling frequency of 25% and a peeling/repair frequency of 0.03, while *T. mortoni* shows 5.5% drilling and a peeling/repair frequency of 0.115. In the Matthews Landing Member of the Upper Palaeocene Porters Creek Formation in Alabama, *T. alabamensis* shows a drilling frequency of 10% and a peeling/repair frequency of 0.03, while *T. aldrichi* is 59% drilled and has a peeling/repair frequency of 0.78. These two species are of similar size, but late whorls of *T. alabamensis* are basally convex while those of *T. aldrichi* are more straight-sided and usually bear a weak adapical carina. Neither species shows pronounced spiral sculpture.

These individual examples (all of which need more detailed study) notwithstanding, there is little convincing evidence that sculpture yields any consistent advantages in resisting predation on turritellines.

Shell geometry is also uncorrelated with peeling and repair frequencies in turritellines; slender and robust species suffer statistically equivalent frequencies. This finding is contrary to Signor's (1985) results for Recent terebrid species in Guam, where robust forms sustained not only much higher rates of both successful and unsuccessful predation than did slender forms, but also higher rates of repair. Slender species are somehow better able to avoid detection or capture by peeling predators. Signor tentatively concludes that smaller aperture size in slender forms is responsible, by preventing access to a crab's cheliped.

It is possible that the turritellid shell shape itself is an adaptation against peeling predation (since it allows deep withdrawal of the body mass); this might help explain its recurrence in a variety of gastropod groups since the Devonian (e.g. Signor 1984).

Two temporal patterns stand out in our results. The first is the Cenozoic and apparent Late Cretaceous stability in predation frequencies. The second is the timing of establishment of this stability. While frequencies of drilling and peeling/repair do fluctuate from the Late Cretaceous to the Recent, none of these changes is significant at the five percent level of confidence. Late

Palaeocene drilling frequencies are approximately as high as those at any other time in the Cenozoic, and modern peeling frequencies are no different from those in the Late Cretaceous. If predation on turritellines did substantially increase, as suggested by previous workers, this increase must have happened prior to the Late Cretaceous.

The low incidence of incomplete drill holes in our total sample (9 of 1097 specimens) is consistent with previous findings (e.g. Vermeij and Dudley 1982), and suggests that, as in most other gastropods, turritellines are not very successful at resisting drilling once subjugated (cf. Vermeij 1982*b*, 1987, p. 210). Late Cretaceous peeling/repair values (text-fig. 3B) are higher than mean values for any epoch in the Cenozoic. This agrees with earlier findings for turritellines and other Cretaceous gastropod groups (Vermeij and Dudley 1982; Vermeij 1987, p. 229).

The overall temporal patterns we see in turritellines agree with patterns observed in some gastropod groups but not in others. As in turritellines, Terebridae show little or no temporal trend in predation frequency during the Cenozoic (Vermeij *et al.* 1980). On the other hand, Conidae display increased incidence of peeling and repair from the Eocene to the Miocene (Vermeij 1987, p. 231). Neither Conidae nor Terebridae have a Cretaceous record (Taylor *et al.* 1980), so if predation significantly affected the evolution of these groups, it did so at varying rates and times.

Vermeij (1977) proposed the 'Mesozoic marine revolution' as an arms race between newly evolved durophagous predators and their prey, and an explanation for the largely Mesozoic appearance of anti-predatory shell structures in many groups of marine invertebrates. Our results for turritellines (and Vermeij's own findings for terebrids) suggest that after the appearance and initial diversification of a prey group, there may be few long-term trends in shell form or structure aimed at resisting drilling or peeling predators. The evolution of anti-predatory shell structures may have occurred relatively rapidly in some prey groups and then advanced no further. In the case of turritellines, any gradual evolution of anti-predatory shell structures, or increase in predation intensity, must have been a completely Mesozoic phenomenon because long-term trends in shell form, sculpture, and predation intensity are absent in the Cenozoic. Any 'arms race' appears to be at a standstill in so far as turritelline shell design is concerned. These conclusions are consistent with previous results (Vermeij *et al.* 1981; Vermeij 1987, pp. 227ff.) that suggested that predation intensities attained essentially modern levels near the end of the Mesozoic, and remained essentially unchanged thereafter.

None of these results contradicts the basic notion of the marine revolution. The history of drilling and peeling/repair in turritellines may suggest that they switched from shell-based defence to behavioural or soft-anatomy defences against predators. Alternatively, both predators and prey may have reached an impasse early on, with neither group able to achieve a morphological breakthrough that might permit a renewal of the race. Although the 'marine revolution' has resulted in many highly armoured prey species, not all of these species have gradually evolved greater predation resistance after their initial appearance.

CONCLUSIONS

We find remarkable stasis in the overall spectrum of shell design in turritellines, a situation mirrored in the absence of temporal trends in the frequency of drilling and peeling attacks on these gastropods. Frequencies of drilling and peeling/repair have not changed significantly since the Late Cretaceous. Unfortunately, low sample sizes in the Cretaceous prevent us from determining exactly when these frequencies reached Cenozoic levels. The strength of shell sculpture is uncorrelated with drilling and peeling/repair frequencies, suggesting that sculpture itself is currently of little value as a predator defence. The lack of correlations between shell form and predation, and the absence of temporal trends in predation intensity, suggest that turritelline shell structure has not evolved continuously in response to predation, at least not during the Cenozoic. Any gradual evolutionary trends in turritelline shell evolution that may have occurred could only have taken place in the Mesozoic.

Acknowledgements. We are grateful to R. L. A. Allmon, M. J. Benton, A. R. Palmer, P. W. Signor, J. D. Taylor, R. D. Turner, G. J. Vermeij and an anonymous reviewer for comments on earlier drafts of the manuscript. This research was supported by grants from the Geological Society of America, Sigma Xi, and the Department of Earth and Planetary Sciences of Harvard University, funds from the Department of Invertebrate Paleontology of the Museum of Comparative Zoology, and a National Science Foundation Graduate Fellowship to WDA. Order of authorship is alphabetical.

APPENDIX 1

Frequencies of drilling and peeling in 27 fossil species of Cenozoic turritellines. All specimens are in the collection of the Department of Invertebrate Paleontology of the Museum of Comparative Zoology.

Species (Age)	Locality	Formation	N	Frequency	
				Drilling (%)	Peeling/ repair
<i>T. abrupta</i> Spieker Miocene	Venezuela	?	23	4	0.00
<i>T. alabamensis</i> Whitfield Palaeocene	Alabama	Porters Creek	30	10	0.03
<i>T. aldrichi</i> Bowles Palaeocene	Alabama	Porters Creek	32	59	0.31
<i>T. altilira</i> Conrad Pliocene	Panama	Gatun	20	25	0.30
<i>T. alveata</i> Conrad Eocene	Mississippi	Moodys Branch	15	13	0.93
Eocene	Louisiana	Moodys Branch	30	60	0.37
<i>T. apicalis</i> Heilprin Pliocene	Florida	Pinecrest	58	17	0.21
<i>T. carinata</i> I. Lea Eocene	Alabama	Gosport	30	13	0.23
<i>T. cumberlandia</i> Conrad Miocene	Maryland	Calvert	15	13	0.33
<i>T. eurynome</i> Whitfield Palaeocene	Alabama	Nanafalia	30	10	0.60
<i>T. femina</i> Stenzel Eocene	Texas	Weches	30	3	0.00
<i>T. gilberti</i> Bowles Palaeocene	Alabama	Bashi	45	29	0.02
<i>T. gladeensis</i> Mansfield Pliocene	Florida	Pinecrest	22	27	0.00
			22	23	0.41
<i>T. humerosa</i> Conrad Palaeocene	Virginia	Aquia	32	25	0.03
<i>T. indenta</i> Conrad Miocene	Maryland	Calvert	18	67	0.17
<i>T. larensis</i> Hodson Miocene	Venezuela	?	50	6	0.06
<i>T. mississippiensis</i> Conrad Oligocene	Mississippi	Byram	30	3	0.03
<i>T. mortoni</i> Conrad Palaeocene	Virginia	Aquia	80	4	0.03
			15	17	0.20

APPENDIX 1 (*cont.*)

Species (Age)	Locality	Formation	N	Frequency	
				Drilling (%)	Peeling/ repair
<i>T. multilira</i> Whitfield					
Palaeocene	Alabama	Tuscahoma	30	7	0.30
Palaeocene	Alabama	Nanafalia	16	0	0.25
			18	6	0.22
<i>T. perattenuata</i> Heilprin					
Pliocene	Florida	Pinecrest	48	2	0.51
<i>T. perdita</i> Conrad					
Eocene	Mississippi	Moodys Branch	30	7	0.13
<i>T. plebeia</i> Conrad					
Miocene	Maryland	Calvert	30	0	0.00
<i>T. pontoni</i> Mansfield					
Pliocene	Florida	Pinecrest	49	31	0.25
			27	37	0.70
<i>T. postmortoni</i> Harris					
Palaeocene	Alabama	Nanafalia	15	0	0.20
<i>T. praecincta</i> Conrad					
Palaeocene	Virginia	Aquia	30	40	0.07
			22	36	0.00
	Alabama	Tuscahoma	7	0	0.29
			4	50	0.75
			19	0	0.05
<i>T. rina</i> Palmer					
Eocene	Alabama	Lisbon	38	13	0.05
<i>T. rubricollis</i> MacNeil					
Oligocene	Mississippi	Mint Spring	15	0	0.07
<i>T. wagneriana</i> Olsson & Harbison					
Pliocene	Florida	Pinecrest	72	19	0.74

APPENDIX 2

Data from previously published sources on drilling and peeling frequencies in fossil and living turritellines.

Species	Age	Locality	N	Drilling (%)
<i>T. acropora</i> Dall	Recent	Bermuda ¹	41	12
<i>T. annulata</i> Kiener	Recent	Ghana ²	436	62.6
<i>T. badensis</i> Sacco	Miocene	Poland ³	1229	17.0
	Miocene	Bulgaria ⁴	1921	40.4
<i>T. banksi</i> Reeve	Recent	Panama ¹	12	16.7
	Recent	Ecuador ¹	9	0
<i>T. berjadinensis</i> Hodson	Miocene	Venezuela ¹	35	9.0
<i>T. bicarinata</i> (Eichwald)	Miocene	Poland ³	112	28.0
<i>T. bieniaszi</i> Friedberger	Miocene	Bulgaria ⁴	532	36.6
' <i>T. carinifera</i> Lamarck'	Eocene	France ⁵	51	14.1

APPENDIX 2 (cont.)

Species	Age	Locality	N	Drilling (%)
<i>T. carinifera</i> Lamarck ¹	Recent	South Africa ¹	6	0
<i>T. communis</i> Risso	Recent	Shetlands ¹	107	11.0
<i>T. erronea</i> Cossmann	Miocene	Poland ³	120	25.0
<i>T. exoleta</i> (Linnaeus)	Recent	Tobago ¹	48	4.3
<i>T. funiculosa</i> Deshayes	Eocene	France ⁵	77	58.4
<i>T. gatunensis</i> Conrad	Pliocene	Panama ¹	70	64.0
<i>T. gonostoma</i> Valenciennes	Recent	Mexico ¹	70	40.0
<i>T. granulata</i> Sowerby	Cretaceous (Albian)	England ⁶	704	3.7
<i>T. howelli</i> Harbison	Cretaceous (Campanian)	Mississippi ¹	83	1.0 (0)*
	Cretaceous (Campanian)	Mississippi ⁷	16	6.3 (0.47)*
<i>T. imbricata</i> Lamarck	Eocene	France ⁵	45	17.8
<i>T. leucostoma</i> Valenciennes	Recent	Mexico ¹	35	26.0
<i>T. mariana</i> Dall	Recent	Mexico ¹	36	36.0
<i>T. mauryana</i> Newton	Eocene	Nigeria ⁸	6	16.7
<i>T. mortoni</i> Conrad	Palaeocene	Virginia ¹	14	7.0
<i>T. nodulosa</i> King & Broderip	Recent	Panama ¹	151	26.0
<i>T. pagoda</i> Reeve	Recent	New Zealand ¹	50	2.0
<i>T. perditia</i> Conrad	Eocene	Mississippi ¹	70	21.0
<i>T. plebeia</i> Conrad	Miocene	Maryland ¹	101	27.7
	Miocene	Maryland ⁹	416	21.0
<i>T. postmortoni</i> Harris	Palaeocene	Alabama ¹	12	0
<i>T. praecincta</i> Conrad	Palaeocene	Alabama ¹	27	0
<i>T. subangulata</i> d'Orbigny	Miocene	Bulgaria ¹	189	21.7
<i>T. symmetrica</i> Hutton	Recent	New Zealand ¹	57	19.3
<i>T. tricarinata</i>	Pliocene	Italy ¹⁰	19	52.6
<i>T. trilira</i> Conrad	Cretaceous (Campanian)	Alabama ¹	13	0
<i>T. triplicata</i> (Brocchi)	Recent	Libya ¹	34	47.1
<i>T. unisulcata</i> Lamarck	Eocene	France ⁵	14	50.0
<i>T. variabilis</i> Conrad	Pliocene	Florida ¹	40	20.0
<i>T. variegata</i> (Linnaeus)	Recent	Gulf of Mexico ¹	53	12.0
<i>T. vertebroides</i> Morton	Cretaceous (Campanian)	Mississippi ¹	11	9.0
<i>T. sp.</i>	Recent	Mozambique ¹	47	19.0
<i>T. sp.</i>	Recent	Philippines ¹	138	68.0
<i>T. sp.</i>	Recent	India ¹	61	10.0
<i>T. sp.</i>	Cretaceous (Campanian)	Mississippi ⁷	17	12.0 (0.41)*
<i>T. sp.</i>	Cretaceous (Campanian)	Mississippi ⁷	13	7.8 (0.69)*
<i>T. sp.</i>	Cretaceous	England ⁶	2	0

Key: ¹Dudley and Vermeij (1978); ²Buchanan (1958); ³Hoffman *et al.* (1974); ⁴Kojumdjieva (1974); ⁵Fischer (1966) ⁶Taylor *et al.* (1983); ⁷Vermeij and Dudley (1982); ⁸Arua (1982); ⁹Kelley (1982); ¹⁰Robba and Ostinelli (1975);

* Percent peeling.

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Typescript received 10 June 1989

Revised typescript received 29 August 1989

A DEDUCTIVE ENQUIRY SYSTEM FOR A PALAEOONTOLOGICAL DATABASE OF MUSEUM MATERIAL

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ABSTRACT. The use of database management systems for cataloguing museum material is becoming widespread. Recent advances in database management systems indicate that in future such systems will have a range of increased facilities, including deductive capabilities and natural language interfaces for casual enquiries. In order to explore some of the consequences of these developments for museum catalogues, a prototype system has been written and examples of its use demonstrated. These show that such systems will have significant research potential in a number of areas in geology in addition to taxonomy.

OUR museums contain a wealth of information which can be used in taxonomic, stratigraphic, palaeoecological and other geological studies. If these valuable resources are to be fully exploited, a sophisticated catalogue system is necessary.

The first catalogues of fossils, or registers of specimens, were usually impressive books containing a list of specimens numbered according to some local system, together with information concerning geographic, stratigraphic and collection details. The entries were made in beautiful copperplate writing but there was little attempt at ordering the entries. To obtain information from such registers is almost impossible unless the registration number of the required material is known. The register might be supplemented by card-index systems, one based on genus, one on stratigraphic horizon, one of type and figured specimens and so on. Such indexes increase the usefulness of museum material, but they are onerous to produce and bulky to store.

During the past twenty years progress has been made towards storing museum catalogue information on computer databases. Price (1984) described how a hierarchical database management system was designed by Cutbill *et al.* (1971) for material in the Sedgwick Museum, Cambridge. Several museums now use improved versions of this early system, such as GOS (Porter 1982, 1983), which was released by the Museums Documentation Association, or a more sophisticated version MUSCAT. Other museums, including Bristol University Museum, use commercially available database management systems, for example the relational databases dBASE III or Oracle. International progress in this field was reviewed by Roberts and Light (1980), and Brunton *et al.* (1985) discuss computing procedures in their *Guidelines for the curation of geological material*.

These systems have enormously increased the availability of information stored in our museums because explicit queries can be made on any attribute recorded in the database, and lists are easily prepared in which specimens are ordered alphabetically on a particular attribute such as name, collector, geographic location or stratigraphic horizon.

Research into database management systems has continued at a high level, and during the past few years advances have been made in several areas including database query languages, user interfaces, deductive databases and recursive query processing. At the same time there has been an increase in the use of remote databases and distributed databases, and many of these developments will be incorporated into the next generation of commercial systems. Much of this work has been done using logic programming languages, in particular Prolog, which have greatly facilitated the construction of prototype systems incorporating some or all of these developments. Thus it is possible to explore the consequences of these advances before commercial systems become widely

available. The relevance of some of these developments has already been recognised in a wide range of disciplines; Rawlings (1988) gives a discussion of applications to molecular biology. Here we investigate the consequences of applying these concepts to the cataloguing of museum material. We describe our experience in designing a prototype system for the large Jurassic ammonites in the University Museum, Bristol, and give some illustrations of the power of such a system in other fields of geology, not just as a museum tool.

PROLOG AND DATABASES

In this section we give a brief explanation of why Prolog is particularly suitable as a research tool in this area; for a full description of the language the reader is referred to one of the many excellent books on the subject, for example Sterling and Shapiro (1986). The recent book edited by Gray and Lucas (1988) gives a good account of recent developments in the use of Prolog in conjunction with databases.

Prolog (programming in logic) is a programming language based on logic and was developed by Colmerauer and his colleagues at Marseille in 1970 (Colmerauer *et al.* 1973). The use of the language has grown rapidly, especially when it became clear in 1981 that logic programming would play a fundamental role in the Japanese Fifth Generation Project. Prolog is now used in a wide variety of applications including expert systems, artificial intelligence, natural language processing, deductive databases and general problem solvers. An example in palaeontology is described by Brough and Alexander (1986) who use Prolog to construct an expert system which provides computer assisted identification of fossils. It has become clear that there is a close relationship between Prolog and relational databases (Gallaire *et al.* 1984), and more generally between Prolog and database query languages. As an example the Prolog predicate

$$f(X,Z) :- g(X,Y), h(Y,Z)$$

has the declarative meaning that $f(X,Z)$ is true for particular values of X and Z if g is true for X and some value Y , and h is true for Y and Z . But in a relational database language this clause has the interpretation that the relation f is the join of relations g and h . Nevertheless, there are major differences between these two approaches. For example, Prolog possesses great flexibility in the data structures it can handle, and allows recursion in both rules and facts. Relational database management systems, on the other hand, have advantages in such areas as updating, efficient handling of transactions, and concurrency.

There is currently a considerable amount of interest in combining these facilities in order to produce a new generation of database query systems. One approach is to use Prolog to construct a 'front end' which transforms a query into a standard form for execution on an existing database management system (DBMS), and an example of this is given in Ghosh *et al.* (1988). Clearly, developments along these lines which allow queries to be formulated in restricted natural language will be of great benefit for casual enquiries to existing databases. Another approach has been to establish deductive database systems containing predicates (or rules) which can be used to produce facts (or tuples) which are not stored explicitly in the database.

In the present work we are examining a prototype system written in Prolog, where the data have come partly from an existing relational database system containing the University of Bristol collection of large ammonites, while the remaining data, the knowledge base, consisting of appropriate chronostratigraphic and ammonite classification schemes and other relevant data, have been entered *ab initio*. The aim is to illustrate, by means of a few examples, the type of query which can be handled and to indicate some of its potential uses. No attempt has been made in this work to produce a natural language front end; as explained above there is intense commercial activity in this area and such products will undoubtedly become widely available in the future.

THE KNOWLEDGE BASE: PROLOG DATA STRUCTURES FOR GEOLOGICAL DATA

General

The particular aspects of geology which are discussed here are chronostratigraphy, palaeontological classification, lithological horizon and locality. These aspects are of two main types. Chronostratigraphic and palaeontological classifications are both attempts to impose order on imperfectly understood phenomena and are of a hierarchical form. They can be represented by a tree structure in Prolog, but the quadtree, a particular form of tree used in geographic information systems (Williams 1988), is too inflexible for the present purpose. The data structures defined in this paper are more general as is necessary to accommodate the complexities of a chronostratigraphic and palaeontological information system. Both classifications have been modified over the years – and will no doubt continue to be modified in the light of future research. In consequence, both types of classification contain many obsolete terms. In contrast, lithological horizon and locality are observed facts. Again, the same stratum or the same outcrop may be known by more than one name, but in each case a name is associated with an observation, not an abstraction.

In the case of the classification schemes, not only is it necessary to define the structures, but also the data must be internally consistent. As noted above, these schemes are continuously evolving. However, in order to maintain internal consistency, it is necessary to choose a scheme and adhere to it. The choice of a classification for a particular taxon or stratigraphic system is a task for a specialist who should ensure that it is modern, widely accepted and readily available in the literature. The Special Reports published by the Geological Society could be an appropriate source for British chronostratigraphy and the Jurassic volumes (Cope, Getty *et al.* 1980; Cope, Duff *et al.* 1980) are selected here for the Jurassic system. The recent revision of the *Treatise on invertebrate paleontology* is used for the ammonite classification (Donovan *et al.* 1981).

Because the lithological horizon and location are factual records, there is not the same problem of internal consistency. In this prototype only one set of lithostratigraphic terms is used at each locality, and no attempt has been made to incorporate a hierarchical classification for lithostratigraphy.

Data structures for chronostratigraphic classification

The chronostratigraphic classification is a tree structure with two additional properties:

1. The sub-trees (which can contain an arbitrary number of elements) are ordered in a time sense, where the latest appears first in the list and the earliest (oldest) last.
2. Each level of the tree is referred to by a descriptor, which is used by geologists as a chronostratigraphic division.

Thus, for example, a small subset of the scheme can be represented as:

Division	Descriptor
cainozoic	erathem
quaternary (LATE ←—— EARLY) tertiary	
	 system
	 series

At the system level, Quaternary is later than Tertiary.

The actual representation used in this report has the following chronostratigraphic divisions (the descriptors):

erathem – system – series – stage – substage – zone – subzone

Each division is not always used. For example, the Aalenian Stage is divided into zones, whereas the Bajocian Stage has two substages, the Upper Bajocian and Lower Bajocian, both of which are divided into zones. The Prolog representation has been chosen so that it can accommodate such

variations of the basic data structure, and accordingly contains three arguments. The first is the name of the node and will be a particular system or series etc. The second is the name (descriptor) of its subdivisions, and the third is a list of those subdivisions with the convention that the elements in the list are ordered, with the latest first and the earliest last. Thus, the general definition is of the form

```
tree(Node,Subdivision,List)
```

and the particular example illustrated above is written as

```
tree(cainozoic,system,[quaternary,tertiary]).
```

A chronostratigraphic scheme based on this representation has been written down to the level of subzone divisions for the Jurassic, using data given in Cope, Getty *et al.* (1980) and Cope, Duff *et al.* (1980).

A further complication in chronostratigraphy is that obsolete terms are met when studying specimens from old collections, or in older literature. The following simple structure is used to incorporate such terms.

```
obsolete(Name,Division,Youngest_division,Oldest_division)
```

where Name is the obsolete name, Division is the chronostratigraphic level in the structure 'tree' of the terms Youngest_division and Oldest_division which are the upper and lower boundaries of Name according to Cope, Getty *et al.* (1980) and Cope, Duff *et al.* (1980). For example, the Prolog fact defining the Charmouthian is written as

```
obsolete(charmouthian,zone,davoci,jamesoni)
```

Using this representation we can now formulate in Prolog several rules of varying complexity which can be used in a query system. Some examples are given below.

1. stratum(Y,X).

This states that Y is a division of X so that for example stratum(quaternary,cainozoic) means that Quaternary is a division of the Cainozoic. The Prolog rule for this is:

```
stratum(Y,X):-tree(X,_L),member(Y,L).
```

The query ?-stratum(Y,cainozoic). will, if asked repeatedly, generate all the divisions of the Cainozoic, while the query ?-stratum(tertiary,X). will produce the single answer

```
X = cainozoic
```

2. substratum(Y,X).

This is similar to stratum(Y,X) defined above except that it spans an arbitrary number of 'generations'. The Prolog definition for this involves two rules:

```
substratum(Y,X):-stratum(Y,X).
substratum(Y,X):-stratum(Y,Z),substratum(Z,X).
```

The query ?-substratum(Y,cainozoic). will, if asked repeatedly, generate all the divisions down to, and including, the level of subzones which are in the Cainozoic Erathem. These rules are useful building blocks to which other rules can be added to formulate powerful queries. For example

```
?-list_x_to_y(X,Y,Lr).
```

lists all the elements, including X and Y, between X and Y, irrespective of the division to which they belong, or their order. Thus

```
?-list_x_to_y(obtusum,bucklandi,L),list(L).
```

will yield the following result

```

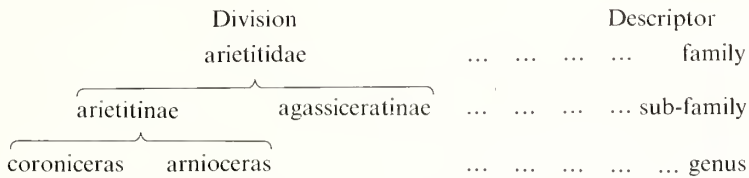
obtusum
turneri
semicostatum
bucklandi

```

even though the *obtusum* Zone is in the Upper Sinemurian and the remaining zones are in the Lower Sinemurian.

Data structures and Prolog representation for palaeontological classification

The palaeontological classification is a tree structure which is similar to that adopted for the chronostratigraphic scheme. The main difference is that the subtrees at each stage are unordered, whereas in the chronostratigraphic case there is a temporal ordering, with the latest first and the earliest last in each subtree. Each level of the tree is referred to by a descriptor, for example order, family, genus etc. A small example of the scheme is given by:



The hierarchical ordering of the levels or taxa is:

suborder – superfamily – family – sub-family – genus – subgenus

Some of these levels are absent in particular cases, so that, for example, a family could be composed of a set of genera. The general Prolog representation is of the form

```
ammclass(Node.Subdivision.List)
```

where Node is the name of a particular palaeontological category and Subdivision is the classificatory level of the items in the list. The small example above is accordingly represented as

```
ammclass(arietitidae,subfamily,[arietitinae,agassiceratinae...]).
```

Using this representation, a query pedigree(X) has been written which will list all the ancestors of the argument X. The Prolog definition of pedigree is

```

pedigree(ammonitina):-!.
pedigree(X):-division(X,D),write(X),tab(3),write(D),nl,stratum(X,Y),pedigree(Y).

```

and the query

```
?-pedigree(arietites).
```

yields the result

```

arietites      subgenus
coroniceras    genus
arietitinae     subfamily
psilocerataceae superfamily

```

An additional complication in the palaeontological classification scheme arises through the

widespread occurrence of synonyms. To deal with this, a further Prolog representation has been introduced of the form

```
synonym(Name,Level,List_of_synonyms)
```

so that for example

```
synonym(schlotheimia,genus,[anguliferites,scannoceras]).
```

indicates that *Anguliferites* and *Scannoceras* are all synonyms of the genus *Schlotheimia*. This structure is used when dealing with specimens which were identified according to earlier classifications.

Link between the chronostratigraphic and palaeontologic classification

The two schemes described are independent, and indeed each is independent of any classification scheme. However, the link between the two is of paramount importance and accordingly a further Prolog structure has been designed to represent this link. This is of the form

```
pal_range(Name,Taxon,Division,Upper_occurrence,Lower_occurrence)
```

As an example of this

```
pal_range(caloceras,genus,zone,lasicus,planorbis).
```

represents the fact that the genus *Caloceras* occurs in the zone range *lasicus* to *planorbis*. It should be noted here that it is only necessary for entries in this category to be made at the generic or subgeneric level; the range for higher categories can easily be derived using simple Prolog constructs.

A query `gen_range` has been written which, by searching both the chronostratigraphic and classificatory trees, lists all genera found in the chronostratigraphic range R1 to R2. The program is as follows

```
gen_range(R1,R2):-list_x_to_y(R1,R2,L),!,pal_range(N,genus,_,X,Y),
    member(X,L),member(Y,L),
    nl,tab(15),write(N),fail.
```

so that for example the query

```
?-gen_range(obtusum,bucklandi).
```

gives the result

```
sulciferites
coroniceras
arnioceras
metarnioceras
tmaegoceras
agassicerias
euagassicerias
asteroceras
aegasteroceras
caenisites
epophioceras
xipheroceras
microderoceras
promicroceras
```


Prolog representation for observed data

The observed data of lithological horizon and location are intimately related, so the two types of information are combined in one data structure.

The general form is

```
place(Grid_easting,Grid_northing,Locality_name,List)
```

List elements are of the form

```
correlation(Lithologic_horizon,Thickness,Chronostratigraphic_division,Upper_occurrence,
Lower_occurrence)
```

The fact

```
place(368300,165000,corston_field_quarry,[correlation(blue_lias,2.4,zone,angulata,angulata)]).
```

records the fact that the outcrop at Corston Field Quarry (368300,165000), consists of 2.4 metres of Blue Lias, all in the *angulata* Zone.

In this Prolog structure, the observed data of the lithological horizons recorded at a section is linked to the chronostratigraphy according to the current interpretation. A revision of this correlation in the light of new evidence can easily be incorporated by a simple modification of the data relating to that section.

Many queries can be asked using the data structures so far described which are of use to geologists in many fields and not only the taxonomist or museum curator.

One such is a query which lists the locations and ranges of a lithostratigraphic unit and its thickness in metres in the overall chronostratigraphic range R1 to R2.

```
?-thick(obtusum,bucklandi,blue_lias).
```

yields

```
saltford_midland_railway_cutting 3 semicostatum bucklandi
kelston_park_quarry 3.93 semicostatum bucklandi
```

This information is essential for the construction of palaeogeographic maps, geologic cross-sections and other visual representations of stratigraphy, and indeed the answers could be transferred directly as data to an appropriate graphics program.

THE DATABASE: DATA STRUCTURE FOR MUSEUM SPECIMENS

The data recorded about each specimen in a catalogue should be a list of facts including horizon, locality and collector and also the subsequent history of the material. A specimen may be moved from one collector or collection to another and it may be identified and cited or figured by several different workers at different times. Each of these events should be noted because they are often important in identifying type material.

In practice it is rare for all these facts to be known about a specimen, particularly if it was collected many years ago and has been moved from collection to collection, but it is often possible to make inferences about its origin and history. For example, if the handwriting on a specimen is recognised as that of a well known collector, it may be assumed that it was collected by that person. These inferences should be clearly noted in the catalogue.

In the prototype described here we make no attempt to create structures to accommodate all the complexities which should be recorded in a museum catalogue. Instead we have selected a few facts, which we assume to be correct, about each specimen so that we can indicate how the museum data can be used in conjunction with the knowledge base. Initially, these facts formed the columns in a

table of a relational database. This information has been transferred into a file and edited into a series of Prolog facts of the form

```
ammonite(V1,V2,V3,V4,V5,V6,V7,V8,V9,V10,V11,V12,V13)
```

where V1 and V2 are identifying numbers, V3,V4 are the generic and specific name, V5 = number of specimens, V6 = matrix, V7 = biological class or order, V8 = size in cm, V9 = stratigraphic system, V10 = horizon, V11 = locality, V12 = geographic region, and V13 = quality of specimen.

The relational database was designed and the ammonite data recorded before the current research was started. No attempt has been made so far to test its Prolog representation for internal consistency, or to ensure that all the terms in the ammonite file are present in the knowledge base. However, with very little editing, it has been possible to search for all specimens belonging to a particular taxon. In this query, the knowledge base is searched and all the members of the same taxon and their synonyms are listed, followed by all such specimens recorded in the database.

In the example, the genus *Schlotheimia* belongs to the family Schlotheimiidae and all the genera in this family and their synonyms are listed. Thus

```
?-taxon(schlotheimia).
```

yields

```
schlotheimia
synonyms are:
  anguliferites
  scamnoceras
```

```
angulaticeras
synonyms are:
  argoceras
  boucaulticeras
etc.
```

```
{the museum specimens belonging to the family Schlotheimiidae are:}
```

```
  28 5001 schlotheimia
   9 5001 schlotheimia
etc.
```

The answer to such a query is invaluable to the taxonomist. Further queries should be constructed which use the horizon and location data from the ammonite structure in conjunction with the knowledge base. The palaeobiologist could easily use these results to test hypotheses which would be very onerous to test by conventional means.

It is pertinent to ask whether the information contained in a computerized museum catalogue is of a quality suitable for research purposes. When using any secondhand material, whether from a museum collection or from published information, the researcher always has to balance the accuracy of the information about a specimen against the availability of alternative specimens and the time and expense of collecting and investigating fresh material.

In a museum catalogue the identification may be wrong, the identifier unknown and the locality and the horizon may have been inferred because of the lithology or some other characteristic feature of the specimen. The computer catalogue should contain all available evidence to enable a researcher to assess the quality of the information about a specimen. Also, if necessary, the specimen itself can be examined.

In the case of published information, it is not always possible to find the source material, particularly referenced material, and in such circumstances future researchers depend entirely upon the professional skill and integrity of the author(s).

SUGGESTIONS FOR FURTHER DEVELOPMENTS

The deductive database described in this paper could form the basis of a powerful information retrieval/on-line query system, but it will need to be extended and developed in several main areas. The knowledge base should be extended to include, for example, all stratigraphic systems and biological phyla. Facilities should be provided so that stratigraphic classifications appropriate to other parts of the world can be incorporated. The structures described in this paper are sufficiently general to achieve this, but the linkage between data from different provinces must be designed with care so that new evidence on correlation can easily be included.

The source of lithostratigraphic information should be added to the description of sections and research, and collection details should be included in the database of museum specimens.

A data entry facility should be provided which checks all new data for consistency and accuracy, as far as this is possible. A 'user-friendly' interface is essential for the casual user and this can be achieved either by a menu-driven query system or a limited natural language processor. The full power of the system described here can only be realized if it is integrated with geologically orientated program packages.

SUMMARY AND CONCLUSIONS

The primary aim of this paper is to show that the valuable information contained in geological museum catalogues can be made readily available for a wide range of investigations. This can be achieved by constructing a knowledge base of geological information and using it in conjunction with a conventional database of museum specimens. The knowledge base itself is an important reference source for many geological investigations. The information in the knowledge base is held in a series of simple Prolog structures which are linked at only a few essential points. Consequently, any modifications which may arise through the availability of new evidence or new interpretations can be made easily, and additional facts can be added without corrupting the existing information.

The geological information included in the conventional museum database can be restricted to observed facts, while the presence of checking routines, although not included in this prototype, would ensure that the internal consistency and accuracy of the database is maintained. This is particularly important when data are entered by relatively unskilled personnel and allows the specialist to concentrate on the complex problems.

The deductive capabilities which are available in the knowledge base allow a more general class of queries to be made than is possible with a conventional database management system.

The results presented in this paper are based on the use of local databases, but it is already clear from the experience currently being gained with remote access to library catalogues that the techniques described here can be extended to include remote databases, both at national and international sites.

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Typescript received 23 November 1988

Revised typescript received 7 November 1989

THE AFFINITIES OF EARLY ONCOCERID NAUTILOIDS FROM THE LOWER ORDOVICIAN OF SPITSBERGEN AND SWEDEN

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ABSTRACT. *Phthanoncoceras oelandense* gen. et sp. nov. from the Kundan (Llanvirn) of Sweden and *Valhallocceras floweri* gen. et sp. nov. from the Cassinian (Arenig) of Ny Friesland, Spitsbergen are described and a new family, the Phthanoncoceratidae (Oncocerida) is proposed. The relationships of the Phthanoncoceratidae to the Oncocerida and Ellesmerocerida are discussed.

COLLECTIONS of Ordovician cephalopods from the lower Kundan of Öland, Sweden (held in the Swedish Museum of Natural History, Stockholm) and from the Cassinian of Ny Friesland, Spitsbergen (made available by Dr R. A. Fortey) contain two genera showing features intermediate between the Ellesmerocerida and the Oncocerida. These genera, *Phthanoncoceras* gen. nov. and *Valhallocceras* gen. nov., possess thick, layered connecting rings and primary siphonal diaphragms, features considered to be characteristic of the predominantly endogastric Ellesmerocerida. However, both these new genera are exogastric, have relatively narrow, marginal to submarginal siphuncles and conch cross-sections which strongly support an affinity with the Oncocerida. Since it is clear that these genera exhibit mixed characters, the presence of an exogastric curvature is here deemed sufficient to assign *Phthanoncoceras* and *Valhallocceras* to the Oncocerida.

The Graciloceratidae were previously thought to represent the most primitive oncocerids. They have thin connecting rings and lack diaphragms. *Phthanoncoceras* and *Valhallocceras* clearly are not graciloceratids, and the family Phthanoncoceratidae fam. nov. is proposed for these two genera. This new family includes the earliest known oncocerids, and exhibits the retention of primitive features more typical of the Ellesmerocerida.

SYSTEMATIC PALAEONTOLOGY

Order ONCOCERIDA Flower *in* Flower and Kummel, 1950

Family PHTHANONCOCERATIDAE nov.

Diagnosis. Exogastric cyrtocoines with depressed to compressed section and a narrow marginal to sub-marginal tubular siphuncle with thickened and layered connecting rings; septal necks orthochoanitic. Siphonal diaphragms present.

Type genus. *Phthanoncoceras* gen. nov.

Remarks. The Phthanoncoceratidae possess primary siphonal diaphragms and thickened, differentiated connecting rings. They therefore should be assigned to the Ellesmerocerida, themselves diagnosed partly on the possession of such structures (Furnish and Glenister 1964, p. K140). However, in their exogastric curvature, combined with the narrow marginal to sub-marginal siphuncle, the two new genera *Phthanoncoceras* and *Valhallocceras* differ from all other ellesmerocerids. Because of these differences, these two genera are placed in the Oncocerida rather

than the Ellesmerocerida. The origin of the Oncocerida is unclear and two possibilities require consideration.

Thickened and differentiated connecting rings are a persistent feature throughout most of the Ellesmerocerida. They are also present in the Proterocameroceratidae of the Endocerida and many tarphycerids, including the Bassleroceratidae. Primary siphonal diaphragms are almost entirely associated with late Cambrian cephalopods as well as the Ellesmeroceratidae and Cyclostomiceratidae of the Ellesmerocerida. The possession of thickened connecting rings combined with the presence of primary siphonal diaphragms may indicate that the Phthanoncoceratidae are related to the Ellesmeroceratidae or Cyclostomiceratidae.

Flower (1964, 1968, 1976) and Sweet *et al.* (1964) considered that the Oncocerida originated from the Bassleroceratidae, but the systematic position of the Bassleroceratidae has been disputed. Flower (*in* Flower and Teichert 1957) and Flower (1964) placed the Bassleroceratidae in the Tarphycerida, but Furnish and Glenister (1964) and Balashov (1962) assigned the family to the Ellesmerocerida. Later Flower (1968) argued that placing the Bassleroceratidae in the Ellesmerocerida broadened that order beyond definition. The present authors agree with this latter view, as the Ellesmerocerida already form a large and diverse order.

The Phthanoncoceratidae are similar to the Bassleroceratidae in possessing thick differentiated connecting rings and an exogastrically curved conch. However, to date, it is unknown whether or not the Bassleroceratidae possess primary siphonal diaphragms. The Phthanoncoceratidae differ from the Bassleroceratidae in their narrower siphuncles and more breviconic, rapidly expanding conchs. In the latter feature the Phthanoncoceratidae are thought to have more in common with the Ellesmeroceratidae and Cyclostomiceratidae.

The Phthanoncoceratidae extend the stratigraphical range of the Oncocerida and also modify the way in which the early evolution of the Oncocerida is viewed (see text-fig. 1). Since there is stratigraphical overlap between the Phthanoncoceratidae, Graciloceratidae and Oncoceratidae, it is not clear when the last originated and this family may have a longer history than currently recognized. The existence of thick-ringed oncocerids in strata as young as the early Kundan may also bring into question the relationship of the Graciloceratidae to later oncocerid families. While it is simpler to derive the Oncoceratidae from the Graciloceratidae (e.g. Flower 1976), the same may not be true for the Valcouroceratidae which possess thick, actinosiphonate connecting rings. If the Valcouroceratidae were derived from the Graciloceratidae the connecting rings would have been secondarily thickened, but, if descended from the Phthanoncoceratidae, a thickened connecting ring was already present. Thus it is possible that the Phthanoncoceratidae may, at different times have given rise to more than one oncocerid lineage.

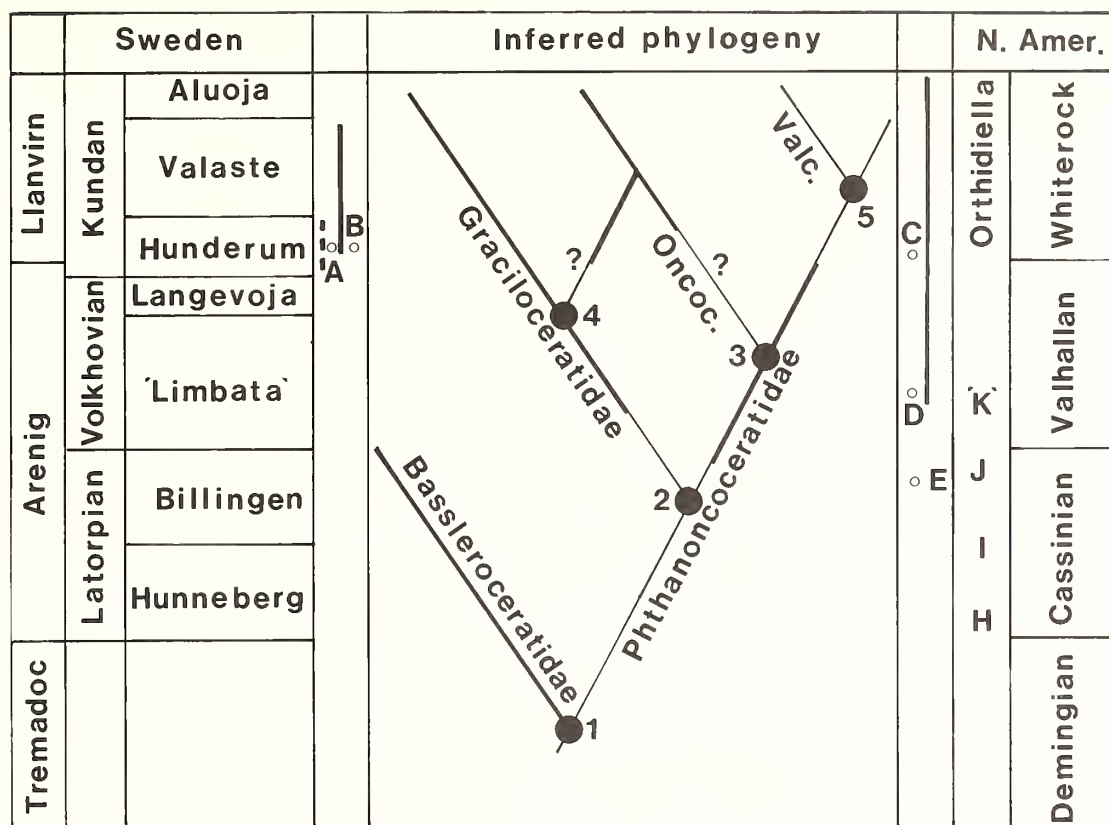
In conclusion, the initial development of the Oncocerida may be the reverse of that which is currently accepted (i.e. derivation from the Bassleroceratidae, e.g. Flower 1976, text-fig. 9) and instead they may have originated from the Ellesmerocerida (quite possibly the Ellesmeroceratidae) through the appearance of exogastric curvature. The Bassleroceratidae and the Tarphycerida formed a lineage derived early in the history of the Phthanoncoceratidae. The Phthanoncoceratidae may themselves have given rise to many of the older oncocerid families through several independent branches (text-fig. 1).

Genus PHTHANONCOCERAS gen. nov.

Type species. Phthanoncoceras oelandense sp. nov.

Diagnosis. Moderately expanding exogastric cyrtocoines; body-chamber slightly inflated adapically with shallow constriction near aperture. Conch section laterally compressed with broadly rounded venter and obtusely rounded dorsum. Siphuncle narrow, tubular and sub-ventral. Septal necks orthochoanitic, connecting rings thick and layered; siphonal diaphragms present apically. External shell smooth, growth lines forming a weak ventral sinus.

Derivation of name. From Greek, *phthanein* = to come before.



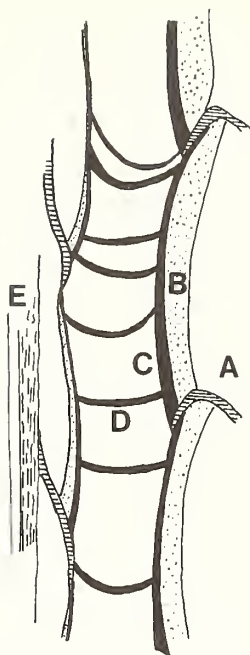
TEXT-FIG. 1. Stratigraphical and phylogenetic relationships of the Phthanoncoceratidae. Chronostratigraphical data based upon Fortey and Bruton (1973), and Jaanusson (1982). Stratigraphical distributions: A, possible range of *Phthanoncoceras oelandense*; B, range of the Graciloceratidae in Öland; C, occurrence of Graciloceratidae (*Leonardoceras* and *Ikesoceras*) in Nevada (Flower 1968); D, occurrence of *Leonardoceras* in Spitsbergen (pers. comm. Dr R. H. Flower to Dr R. A. Fortey 1975); E, occurrence of *Valhallocceras floweri* in Spitsbergen. Synapomorphies: 1, loss of siphonal diaphragms leading to the Bassleroceratidae; 2, loss of siphonal diaphragms and the appearance of thin connecting rings leading to the Graciloceratidae; 3, loss of siphonal diaphragms; appearance of thin connecting rings and development of suborthochoanitic and cyrtchoanitic septal necks (leading to the Oncoceratidae?); 4, appearance of suborthochoanitic and cyrtchoanitic septal necks (leading to the Oncoceratidae?); 5, development of cyrtchoanitic septal necks combined with an actinosiphonate connecting ring leading to the Valcouroceratidae.

Remarks. *Phthanoncoceras* is a monotypic genus, presently recorded only from Sweden. *Oncoceras*, *Beloitoceras*, *Miamoceras* and *Neumatoceras* (all Oncoceratidae) resemble *Phthanoncoceras* in exhibiting similar conch forms and possessing a constriction on the body-chamber. They differ in having suborthochoanitic to cyrtchoanitic septal necks combined with thin connecting rings. *Valhallocceras* differs from *Phthanoncoceras* only with respect to conch section, which in the former is depressed and subtriangular.

Occurrence. Ordovician, Hunderumian (uppermost Arenig to lowermost Llanvirn) of Öland, Sweden.

Phthanoncoceras oelandense sp. nov.

Plate 1, figs. 1-4.; text-fig. 2



TEXT-FIG. 2. *Phthanonoceras oelandense* gen. et sp. nov. Camera lucida drawing of adapical portion of preserved phragmocone of Mo158453 showing details of siphuncle and development of diaphragms. A, septal neck; B, spicular layer of connecting ring; C, nacreous layer of connecting ring; D, diaphragm; E, phragmocone wall. $\times 25$.

Diagnosis. As for genus.

Holotype. Swedish Museum of Natural History, Stockholm, Mo158453, collected by G. Holm in 1894 from the 'glaukonit. grå vaginatunkalk' (lower Kundan) at Hälludden. The species is only known from the holotype.

Derivation of name. From Latin, *oelandense* = from Öland.

Description. The type consists of an exogastric, weakly cyrtocoenic conch with a moderate expansion rate of 20° . The total length preserved is 53 mm, representing the body-chamber and a portion of phragmocone. Adorally the conch section is compressed with a broadly rounded venter and narrowly rounded dorsum; apically the section is less compressed. External shell ornament consists only of very fine growth lines which form a faint ventral sinus.

The body-chamber has a length of 26 mm with adoral and dorsoventral diameters of 16.9 mm and 14.6 mm respectively. A shallow but broad constriction is present on the internal mould 8 mm from the aperture. The body-chamber is slightly inflated adapically.

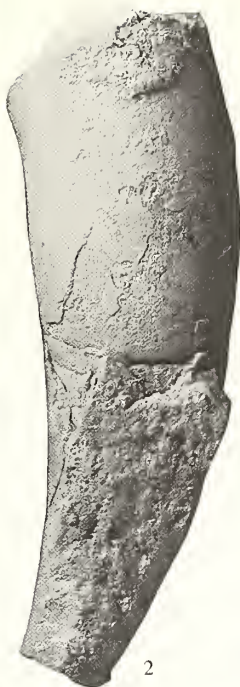
EXPLANATION OF PLATE I

Figs. 1–4, *Phthanonoceras oelandense* gen. et sp. nov. Hunderumian Substage, lower Kundan at Hälludden, northern Öland, Sweden. 1–3, dorsal, left lateral, and ventral aspects of Mo158453, whitened, $\times 1.5$. 4, sagittal section of Mo158453 showing ventral siphuncle, $\times 3.75$.

Figs. 5–11, *Valhallocceras floweri* gen. et sp. nov. Olenidsletta Member of the Valhallfonna Formation. Adjacent to Hinlopenstredet, North Ny Friesland, Spitsbergen. 5–7, dorsal, right-lateral and ventral aspects of PMO NF2276 and 2285, whitened, $\times 1.4$. 8, 'thick' section of NF2276, right-hand side viewed under reflected light showing submarginal ventral siphuncle, $\times 3.5$. 9, apical surface of NF2285 showing depressed subtriangular section and submarginal septal foramen, venter up, $\times 4.4$. 10, details of siphuncle of NF2276 showing short septal necks and thickened connecting rings represented by dark bands, $\times 11.7$. 11, left-hand side of NF2276, apical camerae with siphonal diaphragms crowded into the siphuncle, $\times 11.7$.



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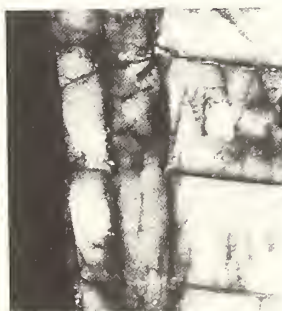
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11

The phragmocone consists of fifteen camerae and has an apicad dorsoventral diameter of 6.9 mm. Sutures exhibit weak dorsal and ventral lobes with corresponding lateral saddles. Cameral depth is 20% of the dorsoventral diameter adapically and 12% adorally where septa are approximated. The siphuncle is narrow (about 15% of the phragmocone diameter) and submarginal (0.5 mm to 1.0 mm from the venter). Septal necks are orthochoanitic and 0.3–0.4 mm long. Connecting rings are tubular and layered. Nine closely spaced diaphragms are present in the siphuncle adjacent to the most adapical camerae (see text-fig. 2).

Occurrence. Hunderumian Substage, lower Kundan (uppermost Arenig to lowermost Llanvirn) at Hälludden, northern Öland, Sweden.

Genus VALHALLOCERAS gen. nov.

Type species. *Valhalloceras floweri* sp. nov.

Diagnosis. Small exogastric conch with subtriangular section, venter obtusely rounded, lateral sides more acutely curved and dorsum broadly rounded. Siphuncle narrow, subventral, orthochoanitic; connecting rings thickened and differentiated; siphonal diaphragms present. Sutures consist of weak dorsal and ventral lobes with lateral saddles. Shell smooth, weak sinus over venter.

Derivation of name. After the Valhallfonna Formation, from which the type species was collected.

Remarks and occurrence. *Valhalloceras* is at present known only from Spitsbergen in facies belonging to the Nileid Association of Fortey (1975). *Valhalloceras* shows many similarities to *Ikesoceras* Flower in terms of gross conch morphology; however, it is unknown whether the latter possesses siphonal diaphragms. The holotype of *Ikesoceras* (Flower 1968, p. 25, pl. 25, figs. 1–5) consists of a body-chamber and the four most adoral camerae, too far adoral to exhibit siphonal diaphragms. The paratype (Flower 1968, pl. 26, figs. 6 and 7) is partly crushed and silicified and represents an adapical portion of phragmocone which, on the basis of *Valhalloceras floweri*, might contain siphonal diaphragms. None have so far been demonstrated. *Valhalloceras* came from a horizon near the top of the Olenidsletta Member of the Valhallfonna Formation, dated as Cassinian J Zone (Cooper and Fortey 1982, fig. 2) and is older than *Ikesoceras* (early Whiterockian zone L *sensu* Cooper and Fortey 1982; Fortey and Owens 1987). *Ikesoceras* appears to occur in a similar facies to *Valhalloceras*, considered to represent the outer lip of the shelf of Ross (1975) and equivalent to the upper slope of Shaw and Fortey (1977), or the Nileid Association of Fortey (1975). Until *Ikesoceras* is better known its systematic position will remain uncertain. However, should *Ikesoceras* prove to possess siphonal diaphragms good reason will exist for regarding it as a senior synonym of *Valhalloceras*.

Valhalloceras floweri sp. nov.

Plate 1, figs. 5–11; text-fig. 3.

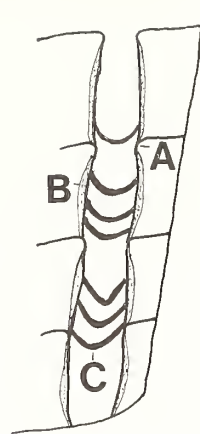
Diagnosis. As for genus.

Holotype. Palaeontological Museum, Oslo NF2276, 2285. These represent complementary fragments of the same specimen. NF2276 was prepared as a thin section, but has been left thick as the siphuncle was displaced in the most apical portion. It was this portion which contained siphonal diaphragms, further preparation of the section would have destroyed these structures. The species is only known from the holotype.

Derivation of name. In honour of the late Dr R. H. Flower.

Description. PMO NF2276 and 2285 represent a portion of phragmocone 44 mm long, slightly crushed adorally. Adapically the cross-section of the conch is almost elliptical with lateral and dorsoventral diameters of 6.4 mm and 5.0 mm respectively. At a position 17.5 mm adorally the cross-section is subtriangular, with the maximum lateral diameter (11.0 mm) 40% of the distance from venter to dorsum (dorso-ventral diameter

TEXT-FIG. 3. *Valhallocceras floweri* gen. et sp. nov. Camera lucida drawing of adapical portion of phragmocone of NF2276 showing details of siphuncle and development of diaphragms. A, septal neck; B, connecting ring; C, diaphragm. $\times 9$.



9.1 mm). A further 15 mm adorally the lateral diameter is estimated to be 16.0 mm. Cameral depth is 17% of the dorsoventral diameter adapically and 13% adorally. The suture comprises weak dorsal and ventral lobes and lateral saddles. Where the conch wall is preserved, it is smooth, consisting of very fine growth lines which trace out a shallow ventral sinus.

The siphuncle is submarginal, its centre being positioned 15% of the distance from the venter to the dorsum; it is 9% of the dorso-ventral diameter. Septal necks are orthochoanitic and about 0.3 mm long. Connecting rings are tubular and consist of two layers; a very thin light coloured dense layer lining the siphonal cavity and a thicker, darker, more diffuse layer forming the cameral side of the connecting ring. In the four most adapical camerae eleven closely spaced diaphragms are present in the siphuncle.

Occurrence. From the outcrop of the Olenidsletta Member between Lundehuken and Papegoyneset, adjacent to Hinlopenstredet, North Ny Friesland, Spitsbergen. The stratigraphical horizon is *c.* 100 m above the base of the Olenidsletta Member of the Vallhålfonna Formation at the top of V_2 in the terminology of Fortey (1980) and Arenig Series Ca 1 in terms of graptolites (= North American *D. bifidus* Zone, see Cooper and Fortey 1982, fig. 2).

Acknowledgements. The authors thank Professor C. H. Holland and Dr J. C. W. Cope for reading early versions of the manuscript. Thanks go to Dr R. A. Fortey for making the Spitsbergen material available and to Professor V. Jaanusson and Dr H. Mutvei for providing the material from Öland. This work was carried out partly under NERC grants GT4/83/GS/135 and GT4/86/GS/137 which are gratefully acknowledged.

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Typescript received 2 May 1989

Revised typescript received 14 July 1989

THE SOLUTE *DENDROCYSTOIDES SCOTICUS* FROM THE UPPER ORDOVICIAN OF SCOTLAND AND THE ANCESTRY OF CHORDATES AND ECHINODERMS

by R. P. S. JEFFERIES

ABSTRACT. A study of the solute *Dendrocystoides scoticus* (Bather), from the Upper Ordovician Ashgill Series, near Girvan, Scotland produces much new anatomical information. The positions of head, tail, the tube feet in the feeding arm, hydropore, gonopore, gonad, pharynx, stomach, anus, brain, left trigeminal ganglion, gill slit (at posterior left in the head), notochord, and tail muscles are deduced. In their basic structure, solutes resemble cornutes, especially the primitive cornute *Ceratocystis*, but differ in retaining a water vascular system, and in other ways. They can be compared in detail with the inferred latest common ancestor of chordates and echinoderms, visualized as resembling the hemichordate *Cephalodiscus* lying on its right side. The tail of solutes is almost certainly homologous with that of cornutes, and therefore with the tail of chordates in general. It is also probably homologous with the locomotory stalk of *Cephalodiscus*. If so, the tail (= stalk) was lost early in the evolution of the Echinodermata, while the water vascular system was lost in the early evolution of the Chordata. The Soluta, if characterized as retaining both a tail and a water vascular system, would therefore have included the latest common ancestor of chordates and echinoderms.

Dendrocystoides scoticus probably belonged to the stem group of the Chordata, on the basis of several advanced features shared with Cornuta including, especially, the posterior left position of the gill slit. The 'carpoids' placed in the group Cincta, on the other hand, probably belonged to the echinoderm stem group but were primitive for echinoderms in possessing a gill slit, located in an anterior, presumably primitive, position like the left gill slit of *Cephalodiscus*. If the tail of solutes is homologous with the tail of cornutes, then the latter organ, contrary to the 'aulacophore' interpretation of Ubaghs, cannot be a feeding arm.

THE aim of this paper is to determine the phylogenetic, and therefore systematic, position of the Soluta. These are a group of strange fossils which are characterized by a feeding arm at one end of the animal and a different appendage (in my view a locomotory tail) at the other end. They have a calcite skeleton of echinoderm type but lack any trace of radial symmetry and for this reason are traditionally placed in the 'carpoid echinoderms'. They are found in marine rocks of Lower Cambrian to Devonian age and comprise 15 described species placed in 13 genera.

I approach the problem of the systematic position of the solutes by a detailed anatomical study of one species, the late Ordovician *Dendrocystoides scoticus* (Bather), chosen because it is abundant in accessible collections. It is the only species in its genus but is very similar to *Dendrocystites* Barrande 1887 from the Ordovician of Czechoslovakia, differing mainly in having a better developed anti-brachial process. My studies convince me that the solutes are built on the same basic plan as the stem-group chordates known as Cornuta. I also believe, however, that the latest common ancestor of the echinoderms and chordates, if it were ever found, would be regarded as a solute. This means that the Soluta, characterized by the possession of a locomotory tail and a feeding arm, straddle the phylogenetic separation between chordates and echinoderms, which gives them the status of an invalid stem group of the Dexiothetica ('unechte Stammgruppe' to use the expression of Hennig 1969). Further work will be needed to decide which of them belong to the true stem group of the Dexiothetica, which of them can be assigned to the stem group of the chordates or of the echinoderms, and which of them, being close in systematic position to the latest common ancestor of chordates and echinoderms, should remain in the nodal group of the Dexiothetica.

The conclusion, presented in this paper, that the solute tail is homologous with the cornute tail, is important to the general morphological interpretation of cornutes, since the solutes possess, in addition to this tail, an appendage clearly homologous with an echinoderm feeding arm. In such case, as Paul (1977, p. 126) pointed out, the cornute tail, contrary to the view of Ubaghs (1968) and Parsley (1988), cannot itself be a feeding arm. In a different direction, I shall argue that the tail of solutes is homologous with the locomotory and prehensile stalk of hemichordates such as *Cephalodiscus*. If so, and if the hemichordates include, or else constitute, the extant sister group of the Dexiothetica, then the latest common ancestor of echinoderms and chordates would have had such a tail. And the echinoderms, as an autapomorphy of the group Echinodermata, would have lost this organ (contrary to the view expressed in Jefferies 1988, p. 11). It follows that the mere possession of a stalk or tail does not characterize an animal as a chordate.

Which way up the solutes lay in life is a matter of dispute. Bather (1913, p. 505) and Caster (1968) oriented the animal with the arm on the left, if the tail is towards the observer, and accordingly spoke of an obverse face (presumably upper) and a reverse face (presumably lower). Kolata, Strimple and Leverson (1977), however, considered it more likely, on functional grounds, that the solutes lay the other way up and used 'aboral' for the presumed upper and 'oral' for the presumed lower surface. I agree with Kolata's orientation of the solutes, partly on functional grounds and partly because it agrees with the likely orientation, accepted by all workers, of the cornutes. I use 'dorsal' for the presumed upper and 'ventral' for the presumed lower surface. These terms, for me, are intended to imply homology with 'dorsal' and 'ventral' in chordates, but not with 'dorsal' and 'ventral' in echinoderms where the terms mean the exact opposite to what they do in chordates (Jefferies, Lewis and Donovan 1987, p. 474). For me, therefore, 'left' and 'right' in solutes mean the opposite of what they did for Caster (1968).

I studied *Dendrocystoides scoticus* by reconstructing it on a drawing board, as with previous studies done in the British Museum (Natural History) (Jefferies 1968, 1969, 1973; Jefferies and Lewis 1978; Jefferies and Prokop 1972; Jefferies *et al.* 1987; Craske and Jefferies 1989; Cripps 1988, 1989a, b, in press). Six different projections (dorsal, ventral, right, left, posterior, anterior) were drawn simultaneously, firstly of the outside and then of the superficial internal anatomy of the animal. The reconstruction was difficult since the fossils, although numerous, are all incomplete. Moreover *D. scoticus* changed shape as it grew and the plating was largely irregular.

The reconstruction of the external shape was largely based on latex casts, but silicone rubber casts were sometimes taken by pressing part and counterpart together against silicone rubber (Wacker RTV-M531 with catalyst T461). The superficial internal anatomy was reconstructed on the basis of internal moulds which, being negatives of the skeleton, can be regarded as positives of the soft parts. The *in vivo* shape of certain parts of the skeleton was reconstructed using large cardboard replicas of the plates and fixing them together with masking tape.

SYSTEMATIC PALAEOLOGY

Superphylum DEUTEROSTOMIA Grobden, 1908
Subsuperphylum DEXIOTHETICA Jefferies, 1979
?Phylum CHORDATA Bateson, 1886

(If a chordate, then stem group of the Chordata)

SOLUTA Jaekel, 1900 (invalid stem group of the Dexiothetica)
Genus *Dendrocystoides* Jaekel 1918
Species *Dendrocystoides scoticus* (Bather 1913)

Remarks. *Dendrocystoides scoticus* is probably a stem-group chordate, as argued below, though at present this conclusion is tentative. It is certain, on the other hand, that *D. scoticus* is a solute, if the Soluta are characterized as a group retaining both a feeding arm and a tail. On the other hand,

the position of the Soluta, straddled across the phylogenetic separation of the Echinodermata and Chordata, makes them an invalid stem group of the Dexiothetica which further research will probably break down. These uncertainties explain the disorderliness of the above systematic 'address'. Ax (1984, 1987) has argued that Linnaean categorial ranks above the species level are arbitrary and ought to be discontinued, except for the genus which is necessary for nomenclatorial reasons. I agree with Ax on this (Craske and Jefferies 1989) and the ranks assigned above are purely traditional (superphylum, phylum) or got by interpolation (subsuperphylum). The group Soluta, set up by Jaekel (1900) as a suborder, is exactly coextensive with the Homoistelea, set up by Gill and Caster (1960) as a subclass and raised by Caster (1968) to the rank of class. Since Linnaean categorial ranks are arbitrary, not real, the difference between Homoistelea and Soluta is purely conventional and the term 'Homoistelea', being younger than 'Soluta', ought to be abandoned.

Dendrocystoides scoticus (Bather 1913)

Plates 1–7; text-figures 2–11, 21

- 1913 *Dendrocystis scotica* Bather; Bather, p. 391.
- 1913 *Dendrocystis scotica*; Woodward, p. 421, 423
- 1918 *Dendrocystoides scoticus* Bather sp.; Jaekel, p. 123.
- 1920 *Dendrocystis scotica*; Hawkins, p. 134.
- 1925 *Dendrocystis scotica*; Bather, p. 5.
- 1928 *Dendrocystis scotica*; Bather, p. 5.
- 1929 *Dendrocystis scotica*; Bather, p. 34.
- 1932 *Dendrocystis scotica*; Hennig, p. 170.
- 1934 *Dendrocystoides scotica* (Bather); Dehm, p. 39.
- 1937 *Dendrocystis scotica*; Woods, p. 175.
- 1938 *Dendrocystis scotica*; Bassler, p. 85, as type species of *Dendrocystoides* Jaekel 1918.
- 1941 *Dendrocystis scotica* Bather; Chauvel, p. 241.
- 1943 *Dendrocystoides scoticus* (Bather); Bassler and Moody, p. 150.
- 1947 *Dendrocystis scotica* Bather; Begg, p. 30.
- 1948 *Dendrocystis scotica*; Cuénot, p. 14.
- 1960 *Dendrocystis scotica*; Špinar, p. 668.
- 1960 *Dendrocystis scotica*; Termier and Termier, p. 87.
- 1965 *Dendrocystoides scotica*; Parsley and Caster, p. 162.
- 1968 *Dendrocystoides scoticus* (Bather); Caster, p. S587.
- 1982 *Dendrocystoides scoticus* (Bather); Meléndez, p. 688.

Comments on synonymy. *Dendrocystoides scoticus* is the only known species of its genus and is also the type species by original designation (Jaekel 1918, p. 123). *Dendrocystis* Bather 1889 is an objective junior synonym of *Dendrocystites* Barrande 1887, of which the type species is *Cystidea sedgwicki* Barrande 1867.

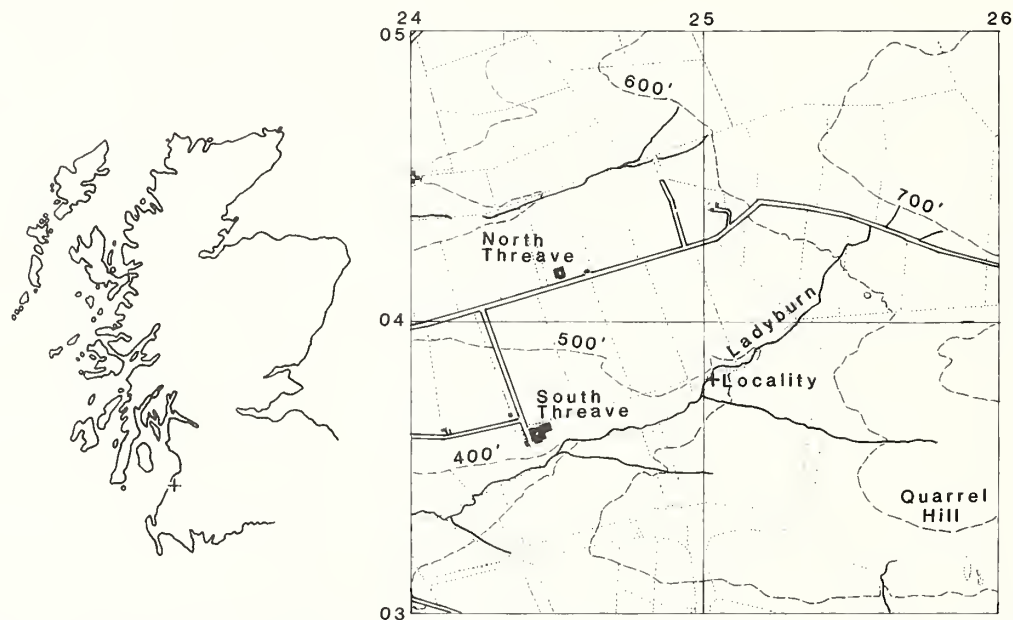
D. scoticus is a famous animal and Bather's reconstruction of it (1913, text-fig. 8, p. 374) has been quoted in many text books and general works without mentioning the trivial name. Such citations are not included in the above list.

History of study. The anatomy of *D. scoticus* has previously been dealt with in two important works: Bather (1913) and Caster (1968). Bather's most notable contribution was to discover the anus for the first time in solutes. Caster was responsible for a number of striking advances: he was the first to discover the pore nodes (hydropore node and gonopore node) in this species and he noted prominences which he called 'horns', though he gave no clear account of their position and relations. He also greatly clarified the systematic situation by distinguishing between *D. scoticus* Bather and the very different solute *Girvanicystis batheri* Caster which occurs in the same bed.

Material. The material examined is as follows: British Museum (Natural History): Gray Collection, E166220–E16223, E23195–E23200, E23202–E23215 (including holotype E23207), E23217–E23231, E23233–E23244, E23246–E23247, E23249–E23255, E23257–E23259, E23289, E23339, E23346–E23348, E23351, E23459, E23461, E23466, E23472, E23700, E23714, E23718, E23759, E23762, E23764, E23765, E23768,

E23769, E28410–E28416, E28418, E28422, E28423, E28426, E28428, E28432–E28435, E28438–E28450, E28452–E28456, E28459, E28460, E28463–E28478, E28481, E28483–E28507, E28511, E28513–E28515, E28517, E28519, E28521–E28529, E28531–E28538, E28540–E28550, E28556, E28557, E28576–E28583, E28585–E28589, E28592–E28596, E28598–E28602, E28760–E28821, E28823, E28825–E28830, E28832–E28836, E28838–E28851, E28853, E28854, E28856–E28860, E28863–E28872, E28874–E28880, E29602–E29609, E52763, E52765, E52870, E62619, E62620, E62622–E62626, E62754, E62755; L. R. M. Cocks Collection, E29365; A. B. Smith Collection, E62521–E62533, E62537; R. P. Tripp Collection, E62778–E62779. Hunterian Museum, Glasgow: E5718, E5719, E5722–E5725, E5729–E5732, E5734–E5736, E5738, E5777, E5778, E5782, E5789, E5792, E5794, E5795, E5797, E5798, E5801–E5803, E5820–E5823, E5826, E5827, E5842, E5856, E5890, E5892, E5893, E5914, E5915, E5947. The total number of specimens examined was 399 and the number of individuals was rather greater than this.

Horizon and locality. All of the specimens examined were from the famous Starfish Bed of the Upper Ordovician Ashgill Series, near Girvan, Scotland. The locality is S6 of Harper (1982, p. 265) which is at National Grid reference NS 2503 0379 on the south bank of the stream called Ladyburn. The valley in which the Ladyburn flows is sometimes called Threave (or Thraive) Glen. For details see Harper (1981, p. 28) and text-fig. 1 herein. This locality is about 8.5 km NE of the church at Girvan (formerly in Ayrshire, now in Strathclyde Region, Scotland).



TEXT-FIG. 1. General position and detailed map of the Starfish Bed locality (S6 of Harper 1982). Locality map traced from Ordnance Survey 1:25000, sheet NS20, Dailly. The dotted lines are field boundaries (stone walls).

According to Harper (1981), the Ladyburn Starfish Bed at this locality is 48 cm thick and divided into three beds (a, b, and c). The lowest of these (Bed a) is 22 cm thick, the famous Starfish Bed of the Gray family and it probably yielded most of the known fossils. Bed b is about 10 cm thick and relatively unfossiliferous, while Bed c is 15 cm thick and contains abundant fossils, though it is not so productive as Bed a. Stratigraphically, the Starfish Bed is near the top of the Farden Member of the South Threave Formation of the Drummuck Group and belongs to the topmost part of the Rawtheyan Stage of the Ashgill Series (Harper 1984, p. 3).

The matrix of the fossils is a greenish silty sandstone. A considerable clay-grade admixture accounts for the good histological detail of the preserved fossils. The calcite of the skeleton of *D. scoticus* has nearly always been dissolved so that the plates are now represented by rust-lined cavities in the rock.

As to conditions of deposition, the beautifully articulated condition of many of the fossils of the Starfish Bed

suggests that they were killed by burial (obration in Seilacher's terminology; see Goldring and Stephenson 1972, p. 612) or perhaps were buried immediately after death. Goldring and Stephenson considered that the Starfish Bed was laid down in shallow water, but Harper (1981) believed that the fossils did not normally live where they are now found, and that the rocks of the Ashgill Series near Girvan were deposited as a turbidite fan at the foot of the continental slope of a continent which lay NW of the lapetus Ocean. This implies that the fossils of the Starfish Bed normally lived on the continental shelf north-west of where they are now found and died when they were carried south-eastwards, downslope and out to sea by turbidity currents.

It seems quite possible that the animals of the Ladyburn Starfish Bed were transported by turbidity currents, as Harper believes, shortly before they died. It seems unlikely that they were usually dead before burial, however. A particular reason for believing that they were killed by burial, as Goldring and Stephenson proposed, is seen in the cornute *Cothurnocystis elizae* (Jefferies 1968, p. 255), where the dorsal and ventral integuments are often separated from each other by a thin layer of rock behind the mouth and right of the strut in the head, but are in contact with each other farther away from the mouth, left of the strut. This suggests that the animal ingested a last mouthful of mud, before being killed. If after death it had then been tumbled about by turbidity currents on the sea floor, it seems almost certain that the mud inside the animal would have become evenly distributed, instead of being preferentially right of the strut as observed. I therefore believe that the articulated fossils of the Starfish Bed, such as *C. elizae* and *D. scoticus*, lived, at least for a few seconds, where they are now found, even if they had been transported downslope by a turbidity current just before death.

ANATOMICAL DESCRIPTION

General morphology

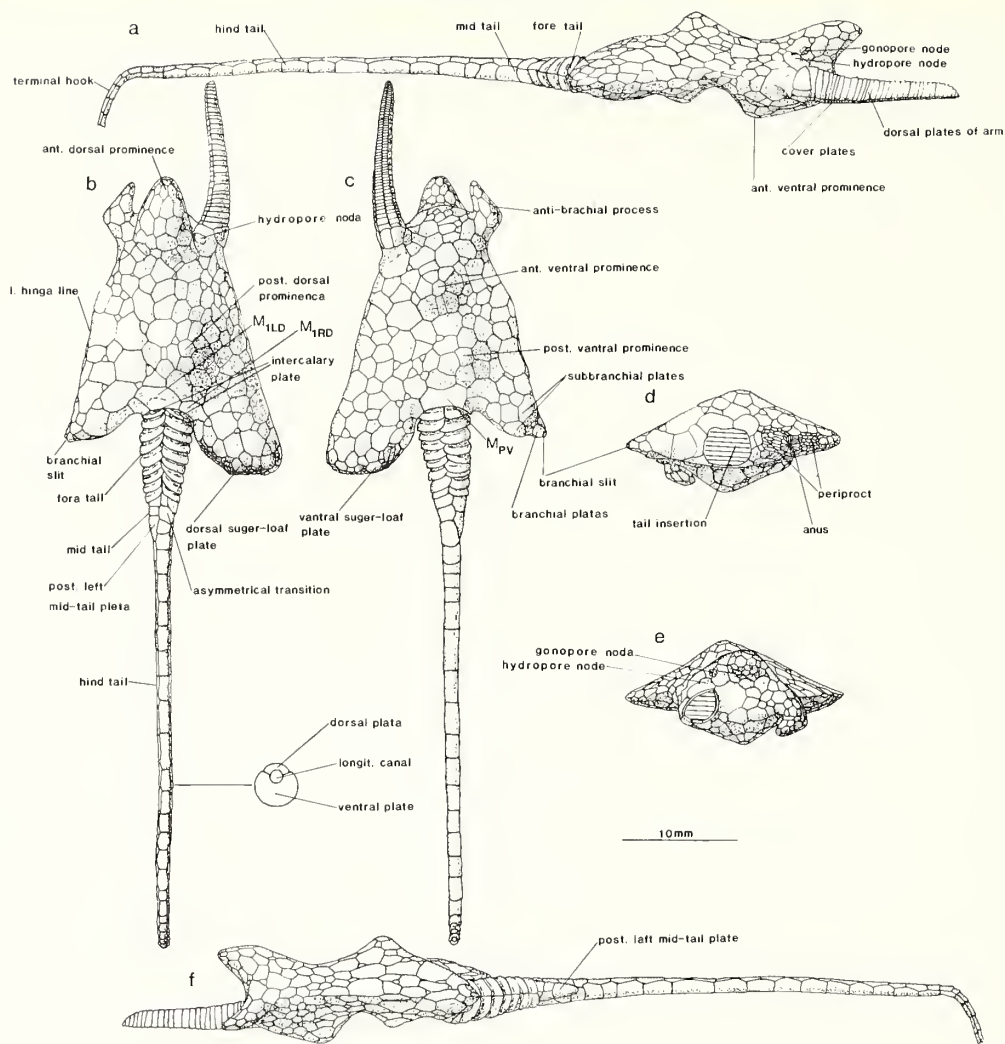
Dendrocystoides scoticus consists of a head, an arm and a tail. In the following description, I shall deal with the external anatomy first and the internal soft-part anatomy later. The main features of *D. scoticus*, in my view, can readily be compared with those of cornutes, as will gradually become clear from what follows. So far as possible, I therefore apply the cornute terminology which I have used in my previous work (see e.g. Jefferies 1986, Chap. 7). In this sense, for example, I use 'right', 'left', 'dorsal', 'ventral', 'anterior', 'posterior' and 'fore tail', 'mid tail' and 'hind tail'. When naming particular plates I use an objective notation, similar to that formerly applied to cornutes and mitrates (e.g. Jefferies 1968). In this notation: CP = cover plate of arm; D = dorsal plate of arm; M = marginal plate (of tail insertion); P = proximal plate of arm base; suffixes _{1,2,3} etc. refer to position in a proximo-distal sequence; suffix _L = left; suffix _R = right; suffix _M = median; suffix _A = anterior; suffix _P = posterior; suffix _D = dorsal; suffix _V = ventral.

The head is trapezium-shaped in dorsal aspect (text-fig. 2). The trapezium is widest near the posterior end of the head and becomes narrower anteriorly. The tail is inserted somewhat left of the middle of the posterior edge.

The size of *D. scoticus* can never be precisely measured in all aspects, partly because the specimens are incomplete and partly because the head was not rigid. One of the best-preserved individuals is E28768 in the BM(NH) (pl. 6, fig. 2). The total length was about 128 mm as preserved (the tail is incomplete), the head width was about 32 mm (the left side is missing), the arm was about 28 mm long, the head length was about 36 mm, and the tail length, so far as preserved, was 76 mm.

External features of the head. The head is approximately, but not accurately, bilaterally symmetrical. The most obvious departures from symmetry are that the arm is at anterior right, an antibrachial process is at anterior left, the right posterior lobe of the head (bearing the anus) is larger and more rounded than the left posterior lobe (the latter bearing, as I believe, a gill slit), and the left side of the head in dorsal aspect shows an obtuse lateral prominence, while no such prominence exists on the right.

The dorsal surface of the head is less flat than the ventral surface, though, in this respect, the difference between the two surfaces is less obvious in very large specimens (on which the reconstruction in text-fig. 2 is based; cf. pl. 1, figs. 1–3, text-fig. 4) than in smaller ones (pl. 1, figs. 4–8, text-fig. 4). On the dorsal surface there are an anterior and a posterior dorsal prominence. The anterior dorsal prominence is situated in the mid line between the base of the arm (on the right) and



TEXT-FIG. 2. *Dendrocystoides scoticus* Bather. Reconstruction of external features: (a) right lateral aspect; (b) dorsal aspect and transverse section of hind tail; (c) ventral; (d) posterior (omitting tail); (e) anterior (omitting arm); (f) left lateral.

the antibrachial process (on the left). In middle-sized individuals it is thimble-shaped and slopes equally in all directions (pl. 1, fig. 5, text-fig. 4). In large individuals, however, it projects strongly forwards, so that its anterior face is actually an overhang and visible in ventral aspect (text-fig. 2; pl. 1, fig. 3, text-fig. 4; pl. 6, figs. 2, 6, text-fig. 9), (text-fig. 2; pl. 1, fig. 3, text-fig. 4; pl. 6, figs. 2, 6, text-fig. 9). The posterior dorsal prominence is situated somewhat right of the mid line. It is capped by a hemispherical plate (pl. 3, fig. 9; text-fig. 6) and usually slopes away from this plate in all directions at about 40°. Like the anterior prominence, the posterior prominence is most obvious in large individuals.

On the ventral surface, there are likewise anterior and posterior prominences. Especially in small and medium-sized individuals, however, these protrude much less than the dorsal prominences (pl. 1, fig. 5, text-fig. 4; pl. 6, fig. 4, text-fig. 9). Their summits approximately underlie the positions of the corresponding dorsal prominences, but are somewhat more posterior. Caster (1968, p. S591)

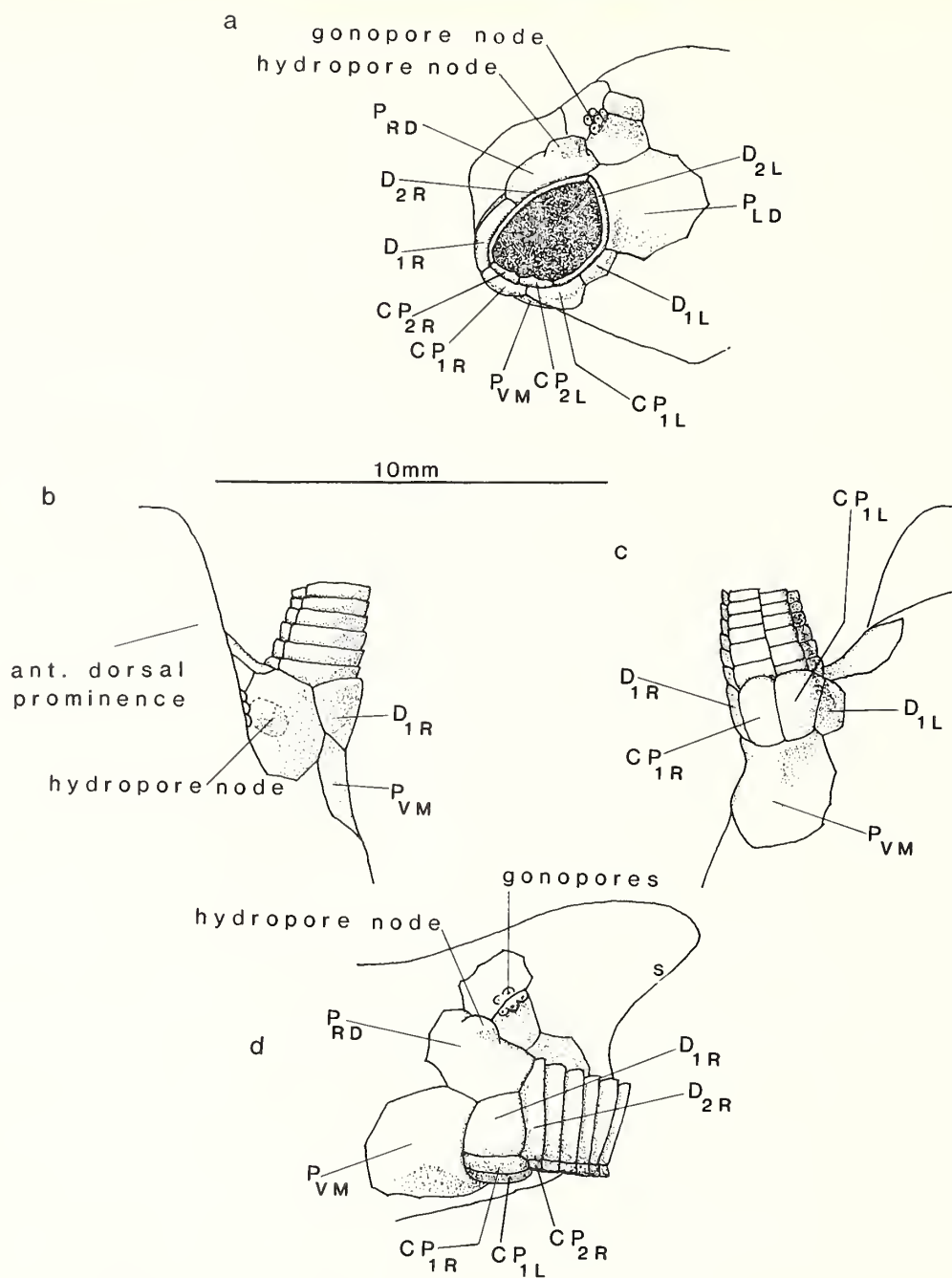
referred to the anterior and posterior ventral prominences respectively as the distal and proximal obverse tumescences.

In transverse section through the head, dorsal and ventral surfaces meet at a sharp angle on the left, posterior to the obtuse lateral prominence already mentioned, and the plates of the respective surfaces meet at this edge along a rather straight line (text-fig. 2; pl. 7, figs. 1–5, text-fig. 10). This line probably functioned as a hinge, allowing the roof of the head to be raised and lowered slightly in this region. On the right side of the head, dorsal and ventral surfaces meet at a rounded contact in transverse section, with no sign of such a hinge.

The plates of the head skeleton are in general unspecialized and irregular. There are, however, some specialized and nameable plates, particularly at the arm base, at the tail insertion, in the anal region right of the tail and in the region of the gill slit left of the tail. These specialized plates will be described below when the respective parts are discussed.

The arm. The arm projects forwards and somewhat downwards from the anterior right extremity of the head (text-fig. 2; pl. 2, fig. 1, text-fig. 5; pl. 6, fig. 2, text-fig. 9). Its skeleton consists of four series of plates – two series of cover plates ventrally and two series of larger ‘flooring’ plates dorsally which, to avoid ambiguity, I shall refer to as dorsal plates. The exact length of the arm cannot be determined because it is never complete in the available specimens. The cover plates are shorter and more numerous than the dorsal plates, except in the proximal part of the arm, and there is no numerical correspondence between dorsal-plate and cover-plate series. The right and left cover plates exactly alternate with each other, whereas the right and left dorsal plates do not. The right and left cover-plate series meet at a smooth curve externally, without interdigitating, though the two series do interdigitate internally where the plates are complexly sculptured. Analogy with echinoderms suggest that the cover plates could open in life so that tube feet could emerge. The right and left dorsal series of plates, on the other hand, would have been flexibly but permanently held together at the dorsal edge of the arm. In transverse section (text-fig. 11e) the arm was not symmetrical for its dorsal edge was consistently leftward of the line of contact of right and left cover plates. The cover plates abut against each other, whereas the dorsal plates imbricate, each one being overlapped posteriorly by its more proximal neighbour. This imbrication would allow the arm to bend in life, especially upwards, rightwards and leftwards.

The plates of the arm-base region, as already mentioned, are specialized (text-fig. 3; pl. 2, fig. 2; pl. 5, figs. 3, 5, 6, text-fig. 8; pl. 6, figs. 5–7, text-fig. 9). The most proximal pair of cover plates, given the notation CP_{1L} and CP_{1R} , are much larger than more distal cover plates, some of which they strongly overlap. Right and left proximal cover plates meet each other at a flat suture and it is fairly certain that they could not open in life. This is shown by a pathological specimen (pl. 6, fig. 7, text-fig. 9) in which an extra plate is inserted distally between the two first cover plates and has formed with them a typical triple junction where the sutures meet at 120° . Such a junction shows that all three plates had always grown in mutual contact, without relative movement. The most proximal pair of dorsal plates (D_{1L} , D_{1R}) make broad contact with the most proximal cover plates, and differ from more distal dorsal plates in not meeting at the dorsal edge of the arm. Indeed, they stop dorsally far short of this edge, since the right one abuts dorsally against the right dorsal proximal plate of the arm base (P_{RD}) and the left one against the left dorsal proximal plate (P_{LD}). A third proximal plate, ventral and somewhat right of median in position with respect to the arm, is named the median ventral proximal plate (P_{VM}). It makes contact anteriorly with the two most proximal cover plates (CP_{1L} , CP_{1R}) and D_{1R} , while dorsally on the right it abuts against P_{RD} . On the left of the arm base, the gap between P_{VM} and P_{LD} is filled, behind D_{1L} , with two or three irregular plates. The right dorsal proximal plate (P_{RD}) carries a boss penetrated by small holes. The histological nature of this boss suggests that it is a node for hydropores (Caster 1968, fig. 372, p. S584) since its porosity resembles the madreporic plate of an echinoid. This suggestion is confirmed by the position of the boss near the mouth, since the latter presumably lay at the base of the arm, and the hydropore is the opening nearest the mouth in cystoids such as *Glyptosphaerites* (Jefferies 1986, fig. 7.18).



TEXT-FIG. 3. *Dendrocystoides scoticus*. External anatomy of arm-base region: (a) anterior aspect (arm omitted distal to D_{2R}); (b) dorsal; (c) ventral; (d) right lateral.

Anterior part of the head. Another set of openings is situated slightly above and left of the hydropore node, at the right base of the anterior dorsal prominence. These openings are variable. Each one is located at the summit of a small paraboloidal calcitic process. The number of these processes ranges from one to about six or seven and they are joined at their bases. The processes, with their pores, are sometimes grouped around the suture between two plates, but sometimes are situated in the middle of a plate. When best developed, the openings are obvious, circular and about 150 μm in diameter (pl. 5, fig. 3, text-fig. 8). Sometimes, however, a circular slight concavity of the same diameter is present at the distal end of a process but is not penetrated by a hole (pl. 5, figs 5, 6, text-fig. 8; pl. 6, fig. 5, text-fig. 9). Such blind processes give the impression that an opening which previously existed had been occluded with skeletal calcite during life. If the mouth was situated at the base of the arm, as seems likely on echinoderm analogies, then the pores now being discussed would be farther from the mouth than the hydropore is, since they do not penetrate one of the standardized plates of the arm base but are situated on, or between, the irregular plates just behind and above these.

The openings at the ends of the paraboloidal processes are probably gonopores. This is suggested by their position, since in cystoids such as *Glyptosphaerites* (Jefferies 1986, fig. 7–18, p. 217) the gonopore is consistently farther away from the mouth than is the hydropore. Also, if the openings were gonopores, their frequent occlusion could represent closure when not reproducing. If these openings were gonopores, then the anterior dorsal prominence of the head, at the base of which their canals emerge, probably represents the position of a gonad. As discussed later, the limits of the gonad seem to show on the surface of the natural internal mould. Despite special search, no feature was observed in these presumed gonopores which might have suggested separate sexes. I therefore cannot say whether this solute was dioecious or hermaphrodite.

The antibrachial process, situated at the left anterior extremity of the head, is, like the dorsal prominences, variable in shape and relative size. It is best developed in the largest specimens as shown in the reconstructions (text-figs. 2, 11) and in pl. 1, fig. 1 (text-fig. 4), and in these specimens it projects downwards, leftwards and forwards from the head. In some smaller specimens it is relatively small and projects leftwards (pl. 1, fig. 7, text-fig. 4). It is more prominent in *D. scoticus* than in any other known species of solute, although Bather (1889) records its presence, more weakly developed, in *Dendrocystites sedgwicki* (Barrande 1867) from the Upper Llandeilo L  tina Formation of Czechoslovakia. By projecting downwards and forwards in *Dendrocystoides scoticus*, its shape and orientation are: (1) grossly the same as the arm, but on the opposite side of the head; and (2) reminiscent of the anterior appendages of cornutes, which probably functioned in locomotion to hinder forward movement and facilitate rearward movement (Jefferies 1986, p. 193). During locomotion, the arm and the antibrachial process of *D. scoticus* may well have functioned in a similar way to these cornute appendages, preventing the head from moving forwards during locomotion and helping it to slide rearwards. The position of the antibrachial process on the left side of the head suggests that it counterbalanced the arm in locomotion, resisting forces acting leftwards and forwards, whereas the arm would resist those acting rightwards and forwards.

The tail. The tail consists of three parts, the fore, the mid and the hind tail, and I believe that these regions are probably homologous with the like-named parts of the cornute tail.

The skeleton of the hind tail (text-fig. 2; pl. 6, figs. 2, 6, text-fig. 9; pl. 7, figs. 1, 2, text-fig. 10) consists of a dorsal and a ventral series of plates which between them enclose a distally tapering canal, circular in transverse section (text-fig. 2b). Except anteriorly towards the mid tail, the plates of the ventral series are thicker walled than those of the dorsal series and occupy much more of the external surface. Because of this, the canal is not central in a transverse section of the hind tail but located entirely dorsal to the centre. Dorsal and ventral plates tend to alternate in position and therefore would have interlocked. Consequently it seems almost certain that, in life, the hind tail was rigid in all directions.

At the posterior end of the hind tail there seems to have been a ventrally-directed rigid hook, ending abruptly, and the axis of the hook is at about 70   to the axis of the rest of the hind tail (text-

fig. 2a, f; pl. 1, fig. 4). In the hook, the dorsal and ventral series of plates are more equally massive than anteriorly and the canal more nearly central in transverse section. A reason for doubt is that the hook as reconstructed is based on a single specimen only and this, as preserved, is not now connected to the rest of the tail. All the other specimens of the hind tail either end abruptly (pl. 6, fig. 6) or else, much more commonly, the tail runs over the edge of the block and is not seen. I believe, however, that the hook probably belongs to *D. scoticus* since it clearly is part of a solute and since Caster (1968, p. S709, fig. 382/4) has published a photograph of a similar terminal hook in *Dendrocystites barrandei* (Bather 1913), a species which in most respects is very similar to *Dendrocystoides scoticus*. Also Ubaghs (in Ubaghs and Robison 1985, figs. 1, 2, 8, 9; text-fig. 16a herein) has recorded a specialized terminal hook, in my view directed ventrally, in the tail of the American Middle Cambrian solute *Castericystis vali* Ubaghs and Robison 1985. Anteriorly in the hind tail of *D. scoticus* the ossicles shorten, both in the dorsal and the ventral series.

In the fore tail (text-fig. 2) the skeleton consisted of major and intercalary plates surrounding a large lumen. The major plates are in four series – right, dorsal and ventral, and left, dorsal and ventral. Each dorsal major plate is united at a suture (pl. 3, fig. 9, text-fig. 6; pl. 7, fig. 7, text-fig. 10) with a ventral major plate on the same side to form a C-shaped element built of two plates. Successive C-shaped elements have curved edges where they meet the dorsal and ventral mid-line of the tail, and these edges overlap, or are overlapped by, those of the C-shaped elements of the opposite side (pl. 3, fig. 9, text-fig. 6; pl. 6, figs. 2, 4, text-fig. 9). The number of C-shaped elements is about nine on both sides. The intercalary plates of the fore tail (pl. 1, fig. 9; pl. 6, fig. 2, text-fig. 9) are small and irregular and were evidently carried in a pliable, small-plated integument which connected the major plates together. They are most obvious near the anterior end of the fore tail, especially at the dorsal and ventral mid-lines. The exact shape of the major plates suggests that the foretail was able to flex, particularly rightwards and leftwards, but also up and down. The lumen of the fore tail was presumably largely filled with muscle and some anticompressional structure, probably a notochord, would be needed to allow flexion without telescoping. The quadriserial skeleton of the fore tail is comparable with that in most cornutes, particularly with the two least crownward of known cornutes *Ceratocystis perneri* and *Protocystites menevensis*, in which right and left ventral plates strongly overlap each other in the ventral mid line (text-fig. 14b; Jefferies 1986, p. 214; Jefferies *et al.* 1987, fig. 10b, p. 442).

The mid tail of *D. scoticus* has a complicated and rather irregular skeleton, transitional between the fore tail and hind tail (text-fig. 2). The dorsal hind-tail series of ossicles can be followed continuously forward into the right dorsal series of major plates in the fore tail (pl. 6, fig. 2, text-fig. 9). And the ventral hind-tail series of ossicles can likewise be followed forward into the right ventral series of major fore-tail plates (pl. 6, fig. 3, text-fig. 9; pl. 7, fig. 1, text-fig. 10). The left side of the mid tail is not comparable for it begins posteriorly with a single half-cone-shaped plate (the posterior left mid-tail plate; pl. 6, fig. 3, text-fig. 9; pl. 7, fig. 1, text-fig. 10) which is neither dorsal nor ventral in position, but left lateral. A dorsal and a ventral plate abut against this anteriorly, and are the posterior members of series leading respectively into the dorsal left and ventral left major plates of the fore tail.

This description of the transition between hind tail and fore tail differs from that of Caster (1968, pp. S583ff.) who considered that, in all solutes, the left ventral hind-tail series passed forward into either the left or right ventral fore-tail series, while the dorsal hind-tail series would pass forward into the diagonally opposite dorsal fore-tail series. In other words, if the ventral hind-tail series passed into the left ventral fore-tail series, then the dorsal hind-tail series would pass forward into the right dorsal fore-tail series and *vice versa*. Perhaps Caster's description is true for some solutes. It does not hold for *D. scoticus*.

Ubaghs (1981) has argued that the tails of solutes are not homologous with those of cornutes and mitrates or, as he would say, the solute stele is not homologous with the cornute and mitrate aulacophore. This assertion reflects his view that the 'aulacophores' of cornutes and mitrates were feeding arms. In accordance with this view, he believes that what he calls the cover plates of cornutes could open to reveal a water-vascular system inside the appendage. (The Ubaghs school

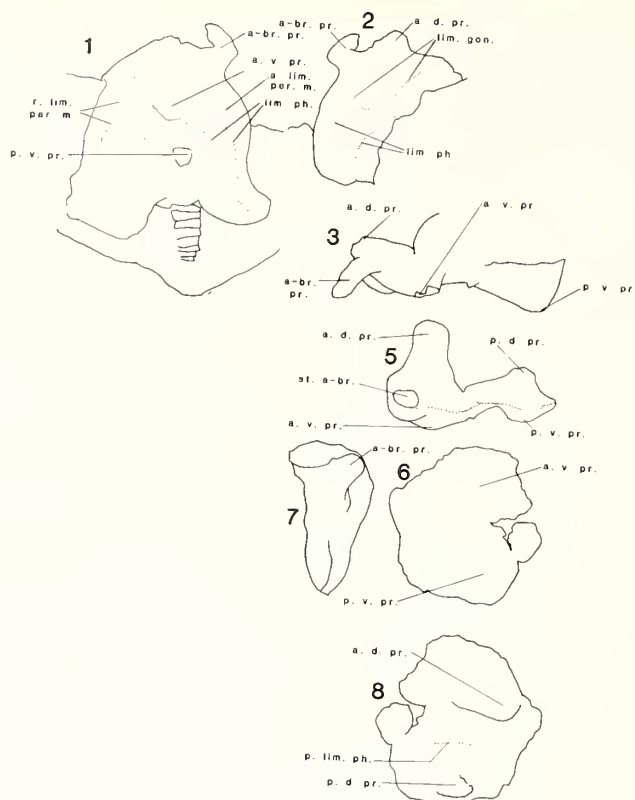
formerly asserted the same of the mitrate 'cover plates' but have since decided that such opening in the mid-line could not happen [Parsley 1982, 1988].) In support of his opinion that the tails of solutes are not homologous with those of cornutes, Ubaghs (1981, p.3ff.) has cited some genuine differences between them: (1) the hind-tail skeleton of solutes consists of an upper and lower series of ossicles, rather than a lower series of ossicles with paired 'cover plates'; (2) the mid-tail skeleton of solutes is made of many somewhat irregular plates whereas the mid tail of cornutes is dominated by a single element, the stylocone, with 'cover plates' above it; and, (3) the canal of the hind tail of solutes expands gradually into the funnel-shaped lumen of the mid tail which passes gradually, in turn, into the broad lumen of the fore tail, whereas in cornutes the lumen of the stylocone is sharply distinct from the canal of the more distal parts of the tail (although continuous with it). In my view these real differences do not show that the tails of solutes, cornutes and mitrates are not basically homologous. They merely show, as might be expected, that these organs are not in all ways the same.

The plates of the tail insertion (text-fig. 2; pl. 7, figs. 6, 7, text-fig. 10) do not seem to be completely standardised and the region was difficult to reconstruct since very few specimens show it in both ventral and dorsal aspect – most of the known specimens of *D. scoticus* are not preserved as part and counterpart. Normally there seem to have been seven plates: two large dorsal plates, which I classify as left and right first dorsal marginals with the notation M_{1LD} and M_{1RD} , one large posterior median ventral plate (M_{PV}), and sometimes two smaller marginal plates on the left and the right, dorsal and ventral to each other – M_{2RD} and M_{RV} on the right and M_{2LD} and M_{LV} on the left. I am doubtful whether these smaller marginal plates always number two on each side, or whether there may not sometimes be one less or one more. The internal structure of the plates of the tail insertion will be discussed below. Caster (1968, p. S592) referred to the plates of the tail insertion as the adsteal girdle.

Posterior part of the head. As to the head openings, the gonopores and hydropores have been described already and the position of the mouth, at the base of the arm, has been implied. Two openings remain to be discussed, the anus on the posterior face of the posterior right lobe of the head, and a gill slit, as I believe, at the end of the posterior left lobe of the head.

I describe the anus first. As already mentioned, it was discovered by Bather (1913, p. 393) in *D. scoticus* for the first time in solutes. It is surrounded by an anal pyramid of long spike-shaped plates and this pyramid is set in a horizontally elongate periproct which was evidently flexible in life, and is armoured with numerous small plates (pl. 5, figs. 2, 4, text-fig. 8). The periproctal plates left of the anus are markedly elongate in a horizontal direction which suggests that the periproct here would sometimes bow outwards as part of a horizontal cylinder, which probably implies that the roof of the head could be pulled here towards the floor. Right of the anal pyramid, the periproctal plates are also horizontally elongate, but not to the same extent, which suggests that the roof here could be depressed, but not so much as left of the pyramid. The frame of the periproct is not well defined, since the integument plates tend to decrease in size towards the periproct. These framing plates tend to be imbricate, whereby the large ones outside the periproct overlap the peripheral plates of the periproct itself. Just to the right of the anus, both dorsally and ventrally, an individualised framing plate larger than its neighbours is present, which Bather called the sugar-loaf plate because of its outline. Hence there are a dorsal and a ventral sugar-loaf plate (pl. 5, figs. 2, 4, text-fig. 8; pl. 6, figs. 2, 3, 6, text-fig. 9; pl. 7, figs. 6, 7, text-fig. 10). At the sugar-loaf plates the frame of the periproct projects posteriorly. Perhaps these two plates helped the anus to protrude posteriorly during defaecation.

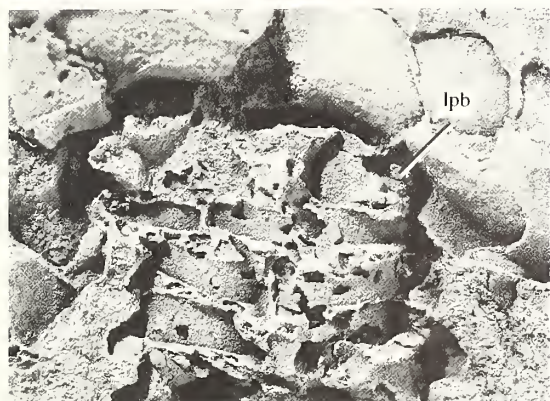
If a gill slit existed in *D. scoticus* we would expect, on cornute analogies, that it would be located near the left posterior angle of the head. As it happens, this region is difficult to reconstruct because few specimens show both part and counterpart and the region has usually been crushed on burial. Some specimens, however, show that there was an area of small plates in this region surrounded by a frame of larger plates (pl. 3, figs. 1, 2, text-fig. 6; pl. 7, fig. 5, text-fig. 10). The frame was made up ventrally of two or three rather thick, ventrally convex plates (subbranchial plates, pl. 3, fig. 2,



TEXT-FIG. 4. *Dendrocystoides scoticus*. Half-scale outline drawings of figs. 1-3 and 5-8 of pl. 1. Each drawing has the same number as the corresponding photograph on the plate; a-br. pr. = antibrachial process; a. d. pr. = anterior dorsal prominence; a. lim. per. m. = anterior limit of peripheral muscle; a. v. pr. = anterior ventral prominence; lim. g. = limit of gonad; lim. ph. = limit of pharynx; p. d. pr. = posterior dorsal process; p. lim. ph. = posterior limit of pharynx; p. v. pr. = posterior ventral process; r. lim. per. m. = right limit of peripheral muscle; st. a-br. = stump of antibrachial process.

EXPLANATION OF PLATE I

Figs. 1-13. *Dendrocystoides scoticus*. 1-3, Hunterian Museum, E5890; $\times 1.2$. Internal mould of head and external mould of part of fore tail; 1, ventral aspect; 2, dorsal aspect; 3, left lateral aspect; see also text-figs. 4/1, 2, 3.4, BM(NH), E29609; $\times 1.2$. Latex of terminal hook of hind tail in left lateral aspect (determination as *D. scoticus* not certain); th = terminal hook; cr = crinoid stem on same block. 5-8, BM(NH) E23339, $\times 2$. Natural internal mould of head (figs. 5-7) and latex of anterior left portion of head (fig. 8). See text-fig. 4 (5-8). The presence of an antibrachial process and the anterior dorsal prominence on one and the same specimen shows that these structures are different. 9, BM(NH) E28529, $\times 5$. Natural internal and external mould of posterior part of head and adjacent fore-tail region in ventral aspect to show, especially, the left pyriform body in ventral aspect (1pb). 10, BM(NH) E28470, $\times 5$. Natural internal mould of posterior part of head and adjacent fore-tail region in ventral aspect to show, especially the brain (br) in undissected condition. 11, BM(NH) E28494, $\times 5$. Natural internal mould of posterior part of head (plate M_{pv}) to show cast of brain in contact with M_{pv} , so far as it can be revealed by dissection. 12, 13, BM(NH) E28416; 12 $\times 2$; 13, detail, $\times 5$. Natural mould, mainly external, of posterior part of head, fore tail and mid tail in dorsal aspect, to show especially the left pyriform body (1pb) as an internal mould.



9

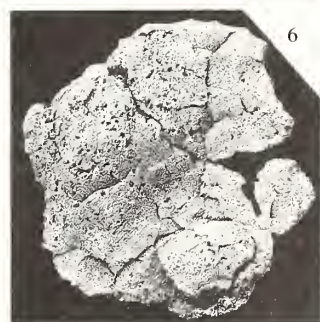


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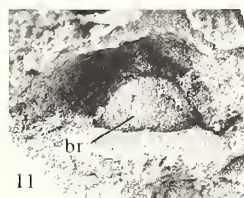


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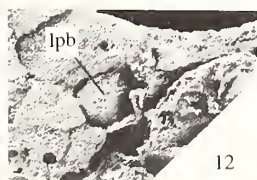
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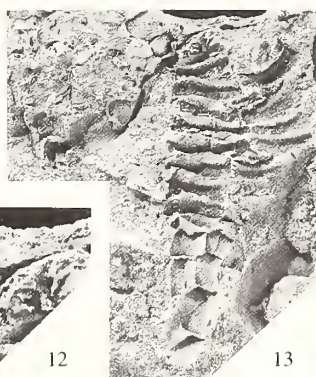
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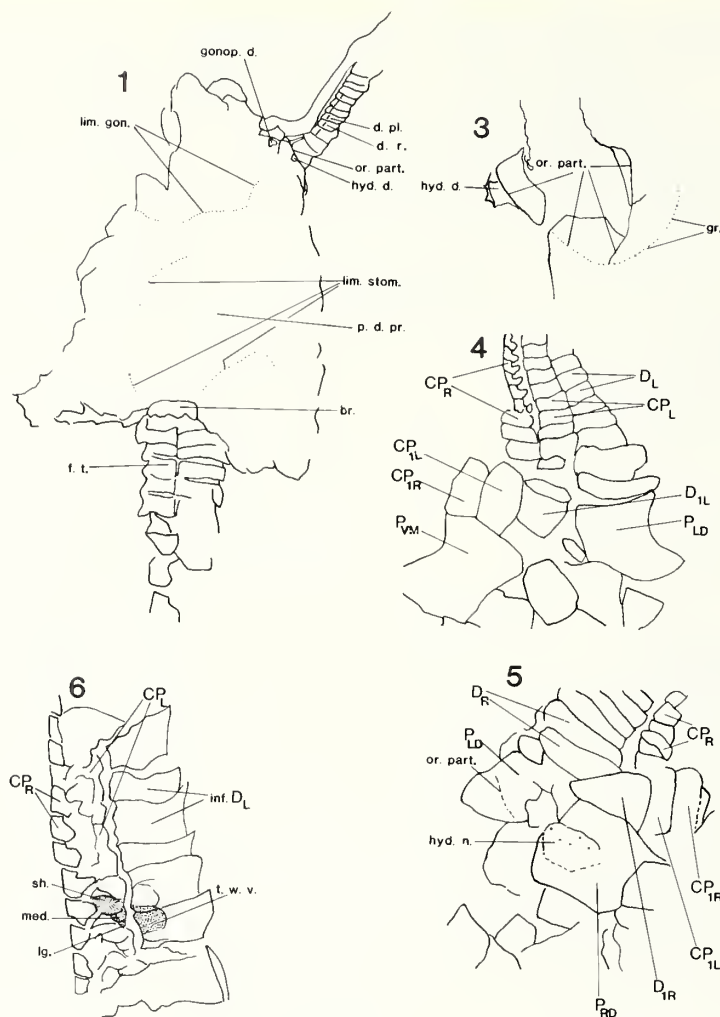
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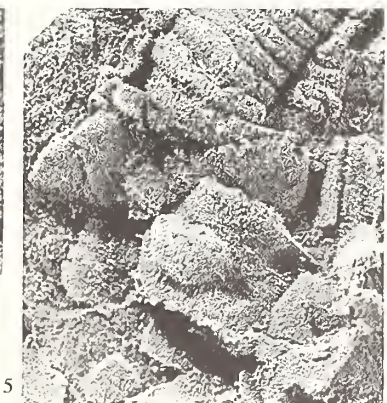
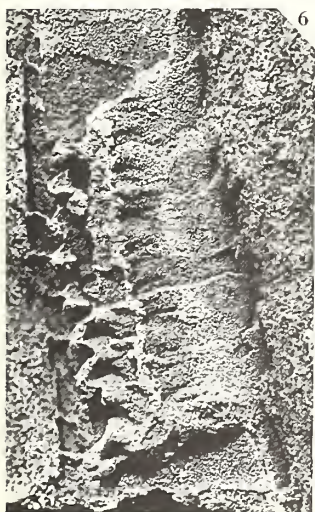
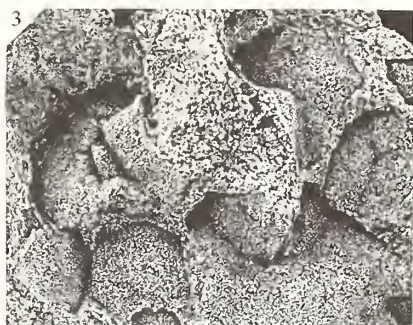
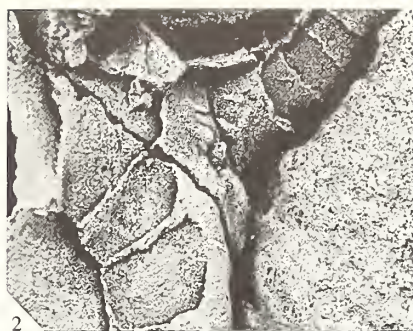
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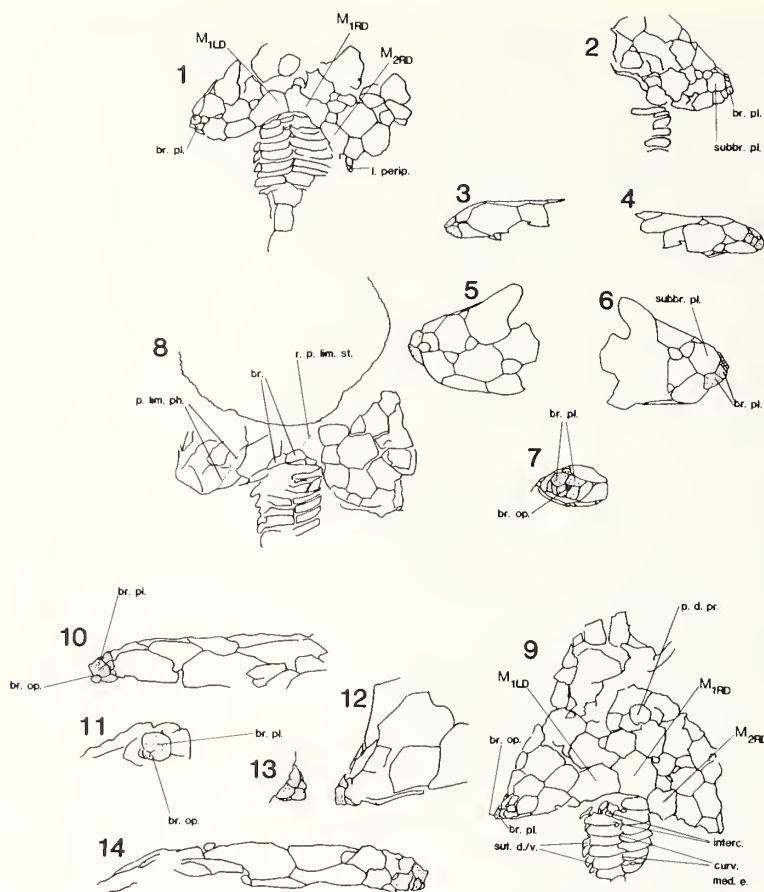
TEXT-FIG. 5. Two-thirds-scale outline drawings of figs. 1 and 3–6 of pl. 2. Each drawing has the same number as the corresponding photograph on the plate; br. = brain; d. pl. = dorsal plate of arm; d. r. = dorsal ridge in infilling of arm; f. t. = fore tail; gonop. d. = gonopore duct; gr. = groove of unknown significance; hyd. d. = hydropore duct; hyd. n. = hydropore node; inf. DL = infilling of left dorsal arm plates; lim. gon. = limit of gonad; lim. stom. = limit of stomach; lg. = long tube foot of a triad; med. = medium-length tube foot of a triad; or. part. = oral partition; p. d. pr. = posterior dorsal prominence; sh. = short tube foot of a triad; t. w. v. = terminal water vessel; C_{PR}, P_{LD}, D_L etc. = plates of arm and arm-base region; cf. text-fig. 3.

EXPLANATION OF PLATE 2

Figs. 1–6. *Dendrocystoides scoticus*. All specimens in BM(NH). Compare text-fig. 5. 1, 2, E28803. 1, Dorsal aspect of natural internal mould of head, arm and fore tail, $\times 2$. 2, arm-base region $\times 5$. 3, E28507, $\times 5$. Natural internal mould of arm-base region in antero-ventral aspect $\times 5$. 4, 5, E28787. Latexes of arm-base region, $\times 5$; 4, ventral aspect. 5, dorsal aspect. 6, 7, E28790. Natural internal mould of arm in ventral aspect to show especially the terminal water vessel and the triads of tube feet. 6, $\times 10$; 7, $\times 40$, to show detail.



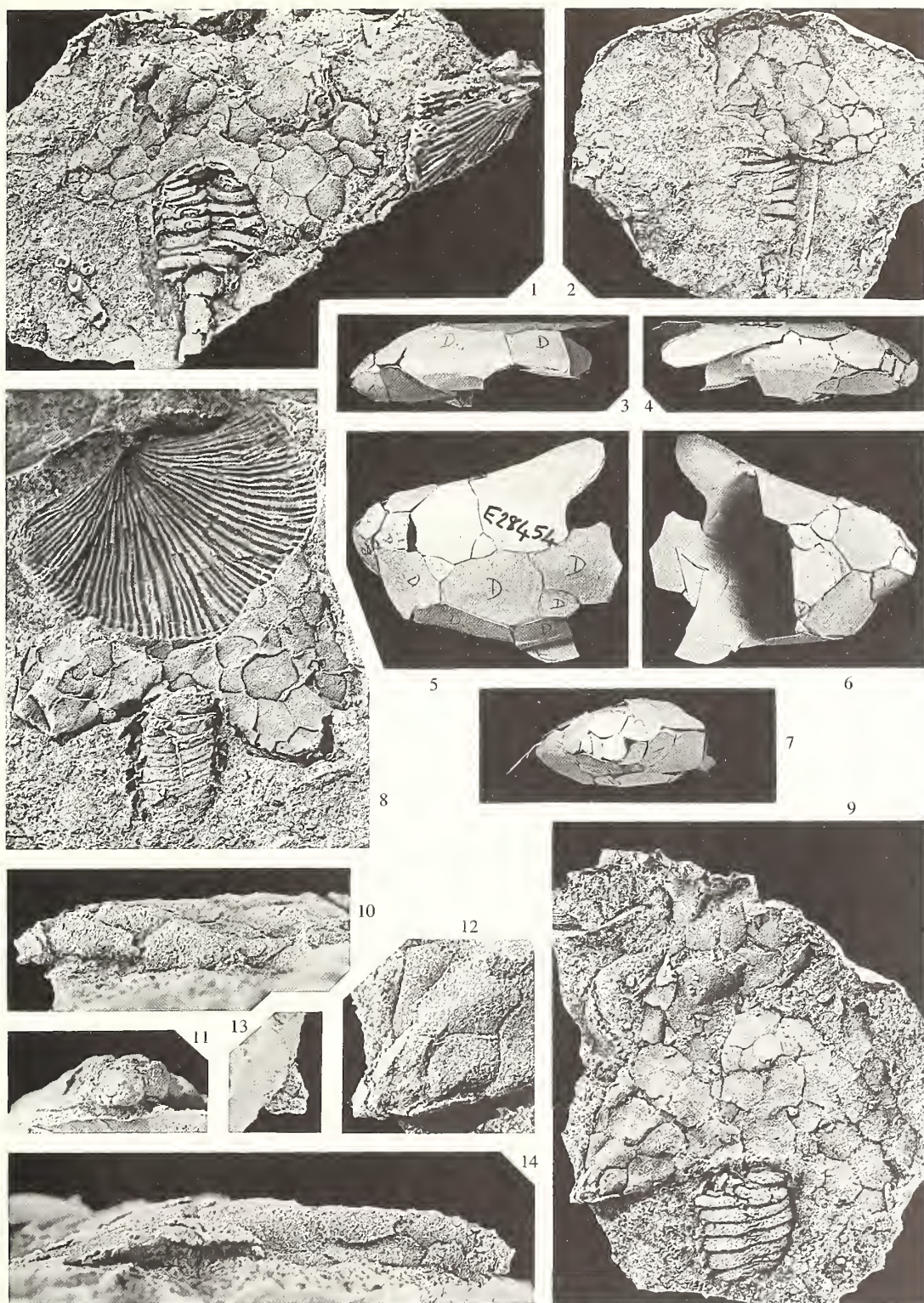
JEFFERIES, *Dendrocystoides scoticus*



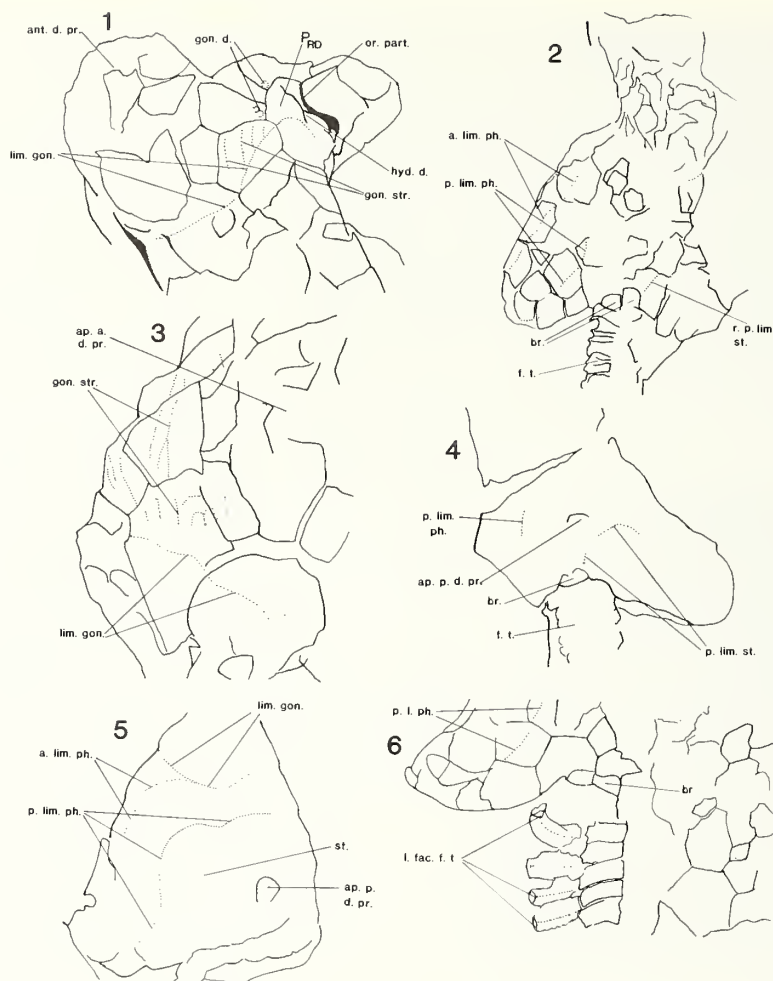
TEXT-FIG. 6. Reduced-scale outline drawings ($\times 0.6$) of pl. 3, figs. 1-14. Each drawing has the same number as the corresponding photograph on the plate; br. = brain; br. op. = branchial opening; br. pl. = branchial plate; curv. med. e. = curved median edge of dorsal plate of fore tail; interc. = intercalary plate of fore tail; l. perip. = left region of periproct; p. lim. ph. = posterior limit of pharynx; r. p. lim. st. = right posterior limit of stomach; subbr. pl. = subbranchial plate; sut. d./v. = suture between dorsal and ventral plate of fore tail; M_{1LD} , M_{1RD} , M_{2RD} = plates of tail insertion; cf. text-fig. 2.

EXPLANATION OF PLATE 3

Figs. 1-14. *Dendrocystoides scoticus*, to show the gill slit (branchial opening) and associated structures. Compare text-fig. 6. Specimens in BM(NH). 1-7, E28454. 1, 2 latexes of dorsal and ventral aspects; $\times 2$; 3-7, cardboard model based on the latexes in figs. 1, 2; $\times 0.36$ of model, c. $\times 4.9$ of specimen. 3, Posterior aspect. 4, Anterior aspect. 5, Dorsal aspect. 6, Ventral aspect. 7, Left lateral aspect. 8-14, E23239. 8, General view of natural mould in dorsal aspect ($\times 2$) and the brachiopod shell which the *Dendrocystoides scoticus* was squashed upon at death - this brachiopod probably explains the inflation with mud of the posterior parts of the head and therefore the good preservation of the branchial region. 9, General view of latex of dorsal surface of head and fore tail ($\times 2$). Figs. 10-14, details of brachial region ($\times 5$). 10, Posterior aspect. 11, Lateral aspect. 12, Dorsal aspect. 13, Ventral aspect. 14, Left antero-lateral aspect.



JEFFERIES, *Dendrocystoides scoticus*



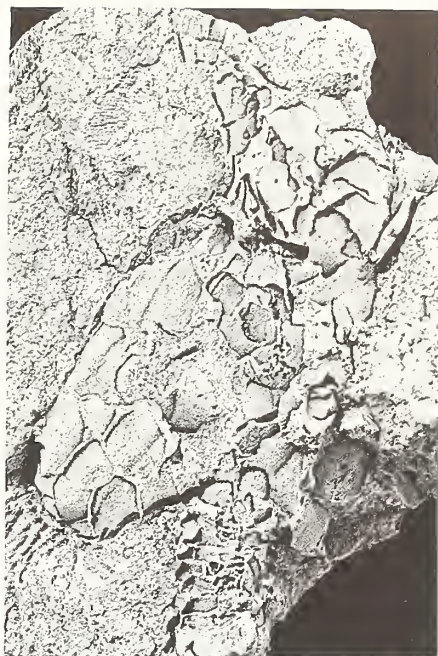
TEXT-FIG. 7. Half-scale outline drawings of pl. 4, figs. 1-6. Each drawing has the same number as the corresponding photograph on the plate; a. lim. ph. = anterior limit of pharynx; ant. d. pr. = anterior dorsal prominence; ap. a. d. pr. = apex of anterior dorsal prominence; ap. p. d. pr. = apex of posterior dorsal prominence; br. = brain; f. t. = fore tail; gon. d. = gonadial duct; gon. str. = gonadial striae on surface of gonad; hyd. d. = hydropore duct; lim. gon. = limit of gonad; l. fac. f. t. = lateral facet of dorsal plate of fore tail (making suture with corresponding ventral plate); or. part. = oral partition; p. lim. ph. = posterior limit of pharynx; p. lim. st. = posterior limit of stomach; r. p. lim. st. = right posterior limit of stomach; st. = stomach.

EXPLANATION OF PLATE 4

Figs. 1-6. *Dendrocystoides scoticus*. Natural internal moulds in dorsal aspect. Compare text-fig. 7. Specimens in BM(NH). 1, E28434, $\times 5$. 2, E28769, Head and foretail $\times 2$. 3, E28532, Left anterior part of head to show gonadial striae $\times 5$. 4, E28601, Right anterior part of head $\times 2$. 5, E23199, Posterior left part of head $\times 2$. 6, E28439, Posterior part of head and fore tail $\times 3$.



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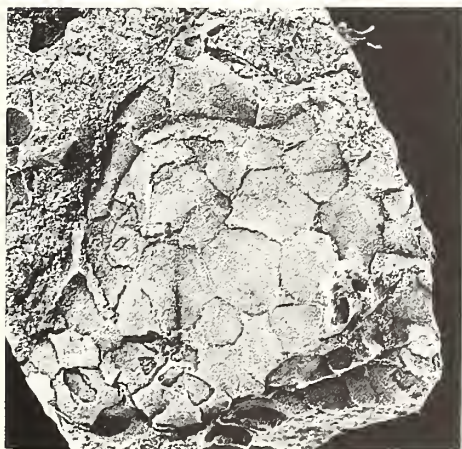
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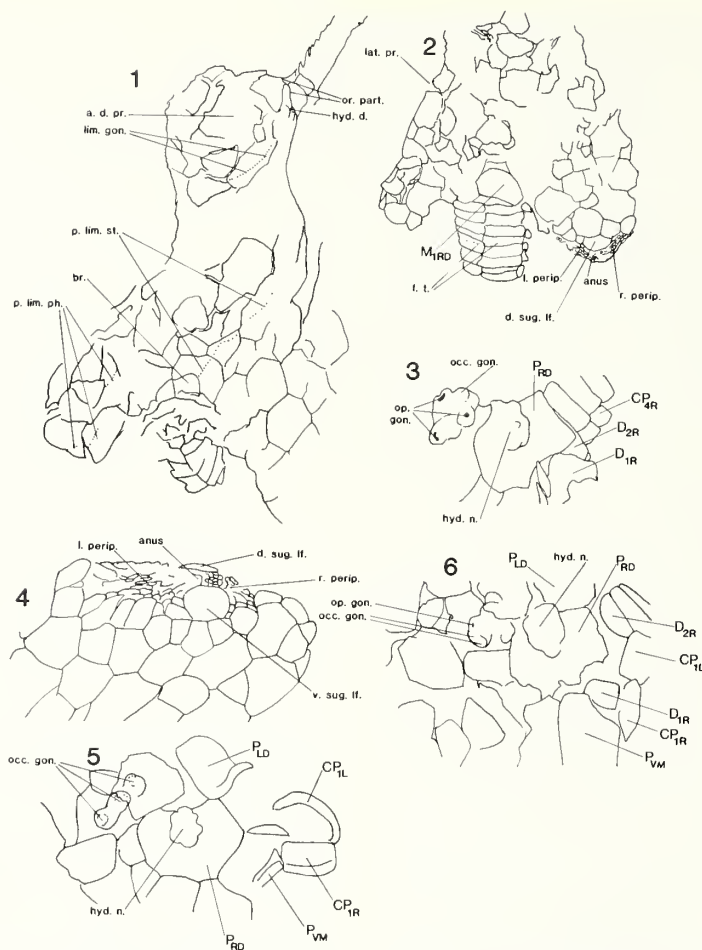
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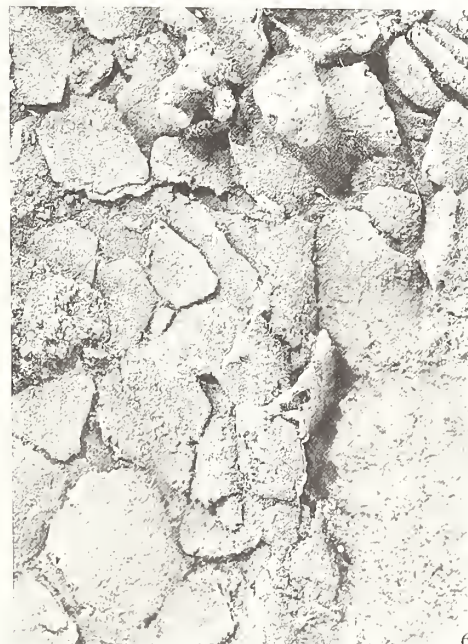
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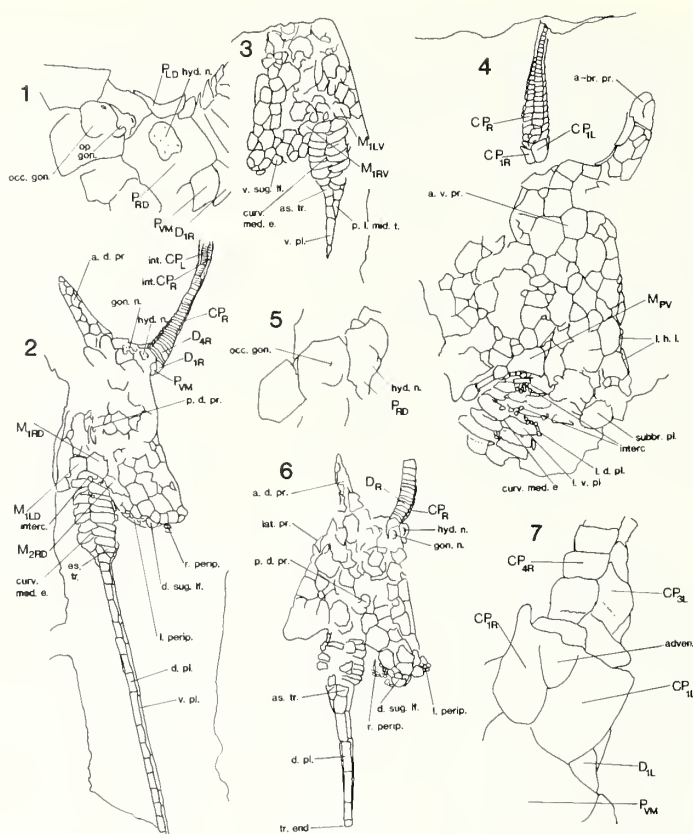


TEXT-FIG. 8. Reduced-scale outline drawings ($\times 0.6$) of pl. 5, figs. 1–6. Each drawing has the same number as the corresponding photographs on the plate; a. d. pr. = anterior dorsal prominence; anus = anus; d. sug. lf. = dorsal sugar-loaf plate; f. t. = fore tail; hyd. d. = hydropore duct; hyd. n. = hydropore node; lat. pr. = lateral prominence; lim. gon. = limit of gonad; l. perip. = left region of periproct; occ. gon. = occluded gonopore; op. gon. = open gonopore; op. part. = oral partition; r. perip. = right region of periproct; v. sug. lf. = ventral sugar loaf; CP_{1L} , M_{1RD} etc. = plates of arm, arm base and tail base as shown in text-figs. 2, 3.

EXPLANATION OF PLATE 5

Figs. 1–6. *Dendrocystoides scoticus*. Compare text-fig. 8. Specimens in BM(NH). 1, E28439, $\times 3$. Natural internal mould of head and fore tail in dorsal aspect. 2, E23229, $\times 2$. Latex of dorsal surface, to show especially the anus, periproct and dorsal sugar-loaf plate. 3, E23219, $\times 5$. Latex of arm-base region with gonopore node and hydropore node; one of the gonopores is occluded. 4, E23237, $\times 5$. Latex of anal region in postero-ventral aspect. 5, E28592, $\times 5$. Latex of arm-base region with gonopore node, hydropore node and the first cover plates in dorsal aspect. The gonopores are all occluded. 6, E23718, $\times 5$. Latex of arm-base region with gonopore node and hydropore node. Some of the gonopores are occluded.

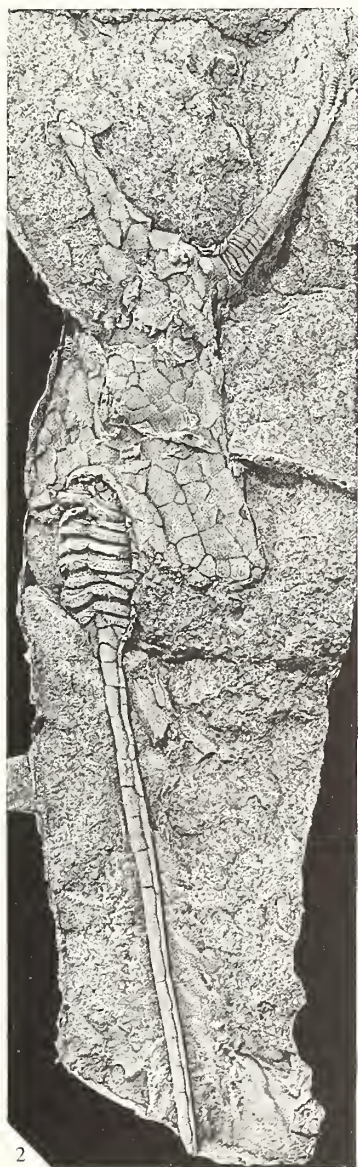


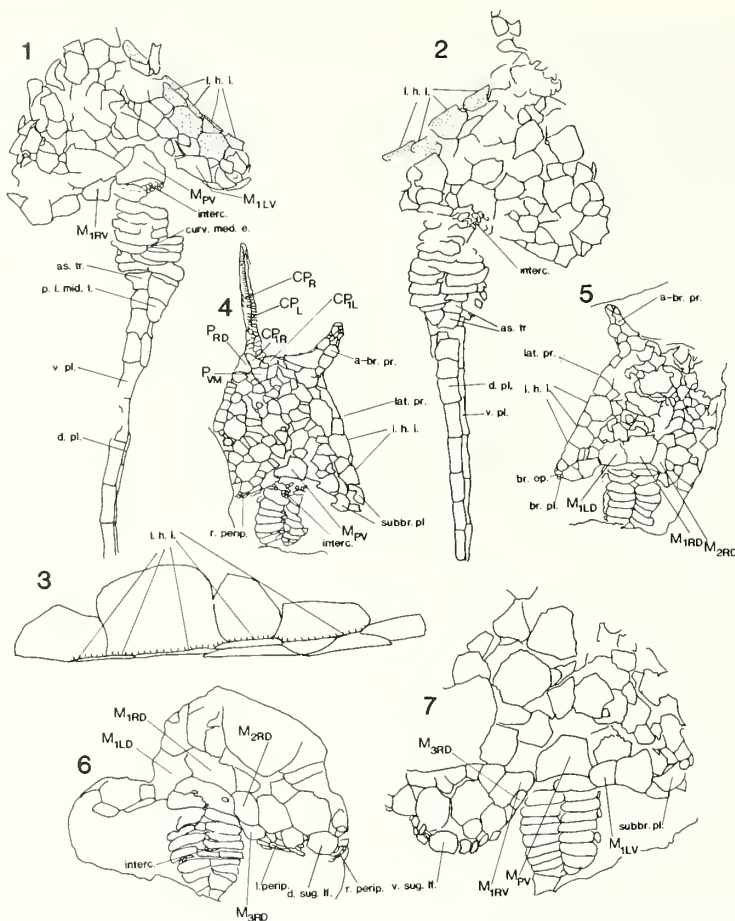


TEXT-FIG. 9. Half-scale outline drawings of pl. 6, figs. 1-7. Each drawing has the same number as the corresponding photograph on the plate; a-br. pr. = antibrachial process; a. d. pr. = anterior dorsal prominence; adven. = adventitious plate between CP_{1L} and CP_{1R} ; as. tr. = asymmetrical transition between mid tail and fore tail; a. v. pr. = anterior ventral prominence; curv. med. e. = curved median edge of dorsal plates of fore tail; d. sug. lf. = dorsal sugar-loaf plate; d. pl. = dorsal plate of hind tail; gon. n. = gonopore node; hyd. n. = hydropore node; int. CPL, int. CPR = interior of left and right cover plates; interc. = intercalary plate of fore tail; lat. pr. = lateral prominence; l. d. pl. = left dorsal plate of fore tail; l. v. pl. = left ventral plate of fore tail; l. perip. = left region of periproct; occ. gon. = occluded gonopore; op. gon. = open gonopore; p. l. mid. t. = posterior left plate of mid tail; p. d. pr. = posterior dorsal prominence; r. perip. = right region of periproct; subbr. pl. = subbranchial plate; tr. end. = truncated end of tail; v. pl. = ventral plate of hind tail; v. sug. lf. = ventral sugar-loaf plate; CP_{1L} , D_{1R} , P_{LD} etc. = plates of arm and arm base (see text-fig. 3); M_{ILD} , M_{PV} etc. = plates of tail insertion (see text-fig. 2).

EXPLANATION OF PLATE 6

Figs. 1-7. *Dendrocystoides scoticus*. Latexes of BM(NH) specimens. Compare text-fig. 9. 1, 2, 3, E28768. 1, Arm-base region, $\times 5$, in dorsal aspect, with the hydropore node and gonopore node; one of the gonopores is occluded. 2, General view in dorsal aspect, $\times 1.2$. 3, ventral aspect, with the asymmetries of the mid tail. 4, E28776, $\times 2$, ventral aspect. 5, 6, E23700, dorsal aspect. 5, Detail of arm-base region, $\times 5$. 6, General view note truncated tail and overhanging dorsal prominence. 7, E28794, $\times 10$. Arm-base region in ventral aspect to show pathological adventitious plate between CP_{1R} and CP_{1L} .

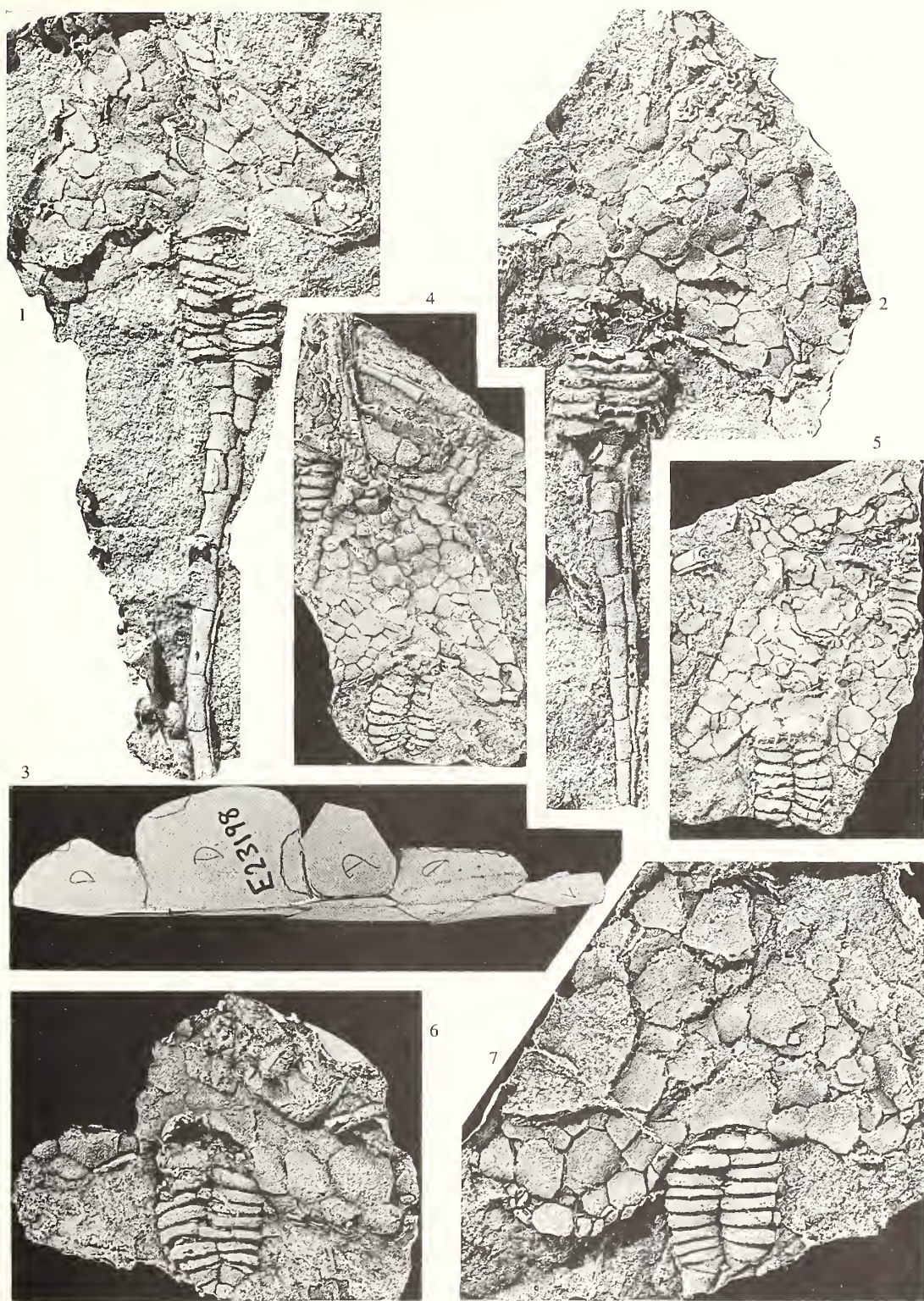




TEXT-FIG. 10. Reduced-scale outline drawings ($\times 0.6$) of pl. 7, figs. 1-7. Each drawing has the same number as the corresponding photograph on the plate: a-br. pr. = antibrachial process; as. tr. = asymmetrical transition between mid tail and fore tail; br. op. = branchial opening (gill slit); br. pl. = branchial plate; curv. med. e. = curved median edge of ventral plate of fore tail; d. pl. = dorsal plate of hind tail; d. sug. lf. = dorsal sugar-loaf plate; interc. = intercalary plate of fore tail; lat. pr. = lateral prominence; l. h. l. = left hinge line; l. perip. = left region of periproct; p. l. mid. t. = posterior left plate of mid tail; r. perip. = right region of periproct; subbr. pl. = subbranchial plate; v. pl. = ventral plate of hind tail; v. sug. lf. = ventral sugar-loaf plate; C_{PR} , P_{RD} etc. = plates of arm and arm insertion (see text-fig. 3); M_{ILD} , M_{PV} etc. = plates of tail insertion (see text-fig. 2).

EXPLANATION OF PLATE 7

Figs. 1-7. *Dendrocystoides scoticus*. BM(NH) specimens. Compare text-fig. 10. 1, 2, 3. E23198. To show structure of presumed left hinge line. 1, Latex of ventral aspect, $\times 2$. 2, Latex of dorsal aspect, $\times 2$. 3, Cardboard model ($\times 0.5 = c. \times 8$ for specimen) of the plates stippled in text-fig. 21/1, 2 to show how the dorsal and ventral plates met at a straight edge - the left hinge line. 4, 5, E23207, holotype, $\times 1.2$. 4, Ventral aspect. 5, Dorsal aspect. 6, 7, E28781. Latex ($\times 2$) of posterior part of head and fore tail, to show especially the plates of the tail insertion. 6, Dorsal aspect. 7, Ventral aspect.



JEFFERIES, *Dendrocystoides scoticus*

text-fig. 6; pl. 6, fig. 4, text-fig. 9; pl. 7, fig. 4, text-fig. 10). These would probably have raised the posterior left angle above the sea floor. Dorsally, the frame consisted of two or three large, rather irregular plates. In one specimen (pl. 3, figs. 8–12, text-fig. 6) the small plates of the posterior left angle of the head seem to be preserved in their proper articulation and form a cone pointing leftwards and rearwards. (Under the anterior part of the head of this specimen there is a large brachiopod – perhaps the mud inside the head was squashed rearwards when the *D. scoticus* fell on top of this shell so that the posterior part of the head was preserved in an unusually inflated condition.) There is no single plate capping the cone. Indeed, the arrangement of the plates seems to be such that a small hole in the skeleton could open between the plates at the tip of the cone (pl. 3, fig. 11, text-fig. 6). I suggest that this small hole represents an outlet opening and, on cornute analogies, that it was a gill slit.

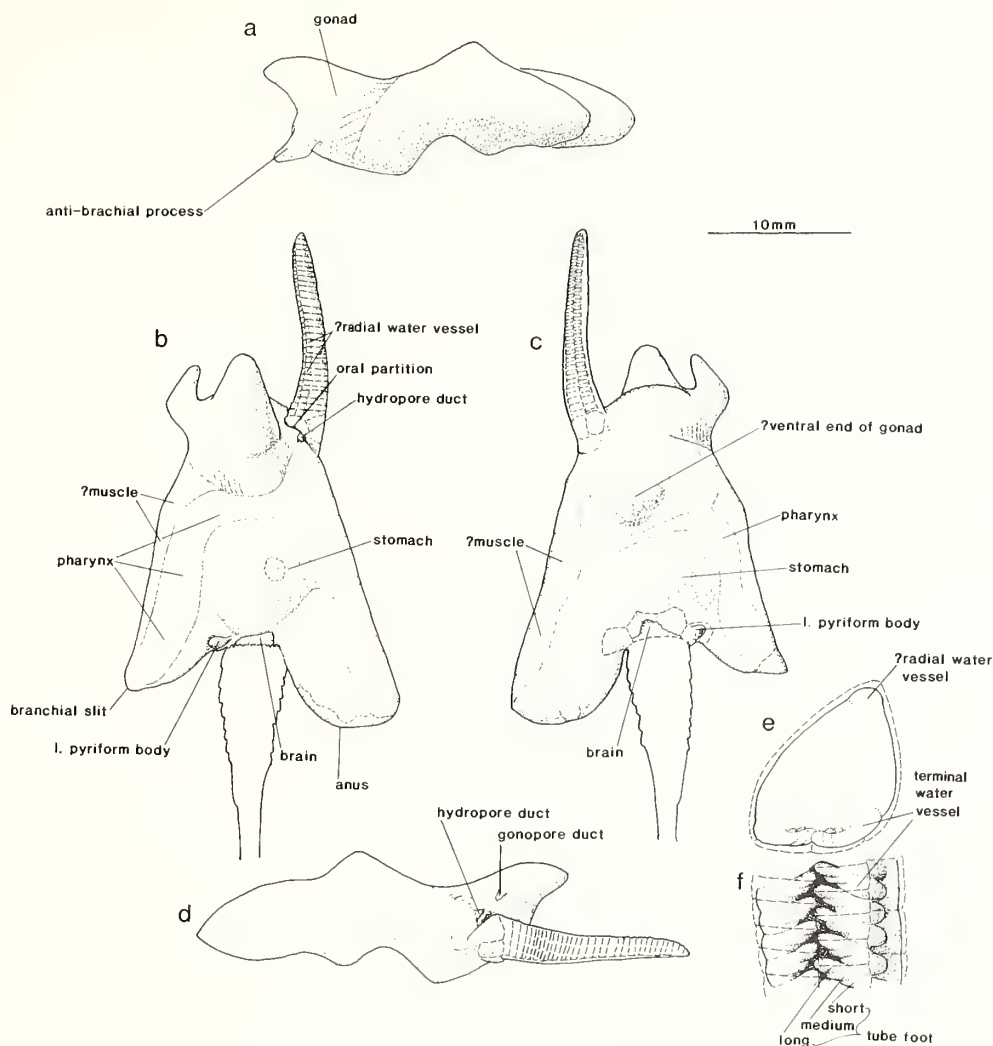
Internal anatomy

A number of grooves and other details can be seen on the internal moulds (text-fig. 11). Such grooves would correspond to ridges on the internal surface of the skeleton but it is more illuminating to consider them as indicating grooves in the surface of the soft parts and thus to use them directly in reconstructing the soft anatomy. Once again, I am influenced, at the outset, by the thought that, in basic plan, *D. scoticus* seems to be similar to the cornute *Ceratocystis*. None of the available specimens showed a complete internal mould. The diagrams of such a mould shown in text-figure 11 are highly composite.

One of the most obvious features in the internal mould is in the arm-base region. Dorsally this feature, called the oral partition (pl. 2, figs. 2, 3, text-fig. 5; pl. 4, fig. 1, text-fig. 7; pl. 5, fig. 1, text-fig. 8), is expressed as a deep groove in the natural internal mould, obliquely transverse to the arm and situated on the inner face of the dorsal arm-base plates P_{LD} and P_{RD} . Ventrally it passes into a shallow groove or break in slope, where it crosses the inner face of plate P_{VM} . In the skeleton, it would correspond to a thin, sharp-topped wall on P_{RD} and P_{LD} which would partly separate the cavity of the arm from the rest of the head. On echinoderm analogies, the arm would contain a radial water vessel and tube feet and was probably used to pick food particles from the mud. Probably the arm would graze food from the mud by sweeping left and right through or over the superficial layer of the sea bottom. If so, the food particles would be passed back towards the base of the arm and there enter the head, through the mouth. The oral partition would delimit the brachial cavity posteriorly and would arch over the mouth.

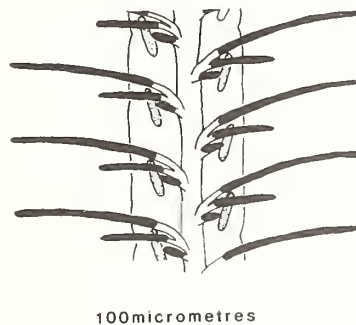
A probable indication of the tube feet is preserved on the ventral surface of the internal mould of the arm (text-fig. 11f; pl. 2, figs. 6, 7, text-fig. 8): such moulds reveal, namely, a series of approximately sausage-shaped structures equal in number to the cover plates. In the terminology which I shall adopt, the proximal end of the sausage is situated where the latter makes contact with the dorsal plate, at right or left of the arm, while the distal end is near the median line of the arm. Each sausage is obliquely disposed so that its distal end is anterior to its proximal end. The long axis of the sausage runs diagonally across the relevant cover plate. The sausage itself overlaps distally on to the next cover plate anterior, near to the median line of the arm, while proximally it overlaps on to the next cover plate posterior, away from the median line of the arm. The distal part of each sausage is divided into three lobes by two grooves which run transverse to the length of the arm. Because of these grooves, each sausage is clearly divided into three lobes towards its distal end.

A comparison of these structures with the tube feet of some crinoids is suggestive. Thus in many crinoids, such as *Antedon* (Nichols 1960), the tube feet are arranged in groups of three (text-fig. 12), each group arising from a terminal water vessel which itself branches from the radial water vessel. The three tube feet of a group differ in length, there being a long one distally, a short one proximally, and a medium-length one between the two others ('distally' and 'proximally' here refer to the position in the pinnule of the crinoid). The short and medium tube feet are in contact externally with a fold of soft tissue which is called a lappet and contains an ambulacral plate (a cover plate), whereas the long tube feet emerge between successive lappets. The lappets open when the tube feet in contact with them expand and they close when these tube feet contract. Because of their contained



TEXT-FIG. 11. *Dendrocystoides scoticus*. Reconstructed internal mould representing the superficial anatomy of the soft parts: (a) left lateral aspect of head; (b) dorsal; (c) ventral; (d) right lateral; (e) transverse section, seen from in front, of an arm near, but not at, its base; (f) soft parts of arm in ventral aspect.

TEXT-FIG. 12. The tube feet of the crinoid *Antedon bifida* in oral aspect (after Nichols 1960, text fig. 1, modified), corresponding to the ventral aspect of *Dendrocystoides*. Note the arrangement of the tube feet (black) in triads, each with a long, a medium and a short tube foot, and the relation of the triads to the cover plates (dotted) and to the radial and terminal water vessels.



musculature, the long tube feet can contract suddenly towards the ambulacral groove, the medium tube feet can contract suddenly towards or away from the groove, and the short tube feet can move in any direction. Paul and Smith (1984) have suggested that primitive echinoderms such as edrioasteroids could open the ambulacral plates or plating by pushing with their tube feet against the adradial faces of these plates, very much as crinoids do. The surfaces of the tube feet of crinoids are provided with sensitive outgrowths called papillae which, when stimulated, squirt out a stream of mucus to entangle microscopic prey. Such prey particles will normally bump first into the papillae of the long tube feet and, when once entangled, will then be passed to the medium tube feet, and from there to the short tube feet which will hand them, still wrapped in mucus, onto the ciliated tract of the ambulacral groove. By the beat of cilia in this groove, they will then be carried to the mouth.

The sausage-shaped structures observed in *D. scoticus* may each correspond to the terminal water tube of a crinoid, together with the three attached tube feet. The three terminal lobes of the sausage would, in such case, correspond to the three tube feet of a group – short, medium and long. If this suggestion is correct, then the long tube foot, as in crinoids, will be the most distal member of its group (distal with respect to the arm), the medium tube foot will be in the middle of the group, and the short tube foot will be the most proximal. Moreover, as in crinoids, the longest tube foot will coincide in position with the contact between successive cover plates (lappets) whereas the short and medium tube foot will be in contact with the inner surface of the main part of a cover plate. Presumably the cover plate would open when the contiguous terminal water tube distended. These various correspondences seem too complex to be accidental and suggest that we are dealing here with genuine homologues. If so, then the grouping of tube feet into triads, and their observed relationship to cover plates, would probably be primitive for echinoderms, and this is true whether *D. scoticus* is a stem-group chordate (as is likely) or a stem-group dextiothete or even a stem-group echinoderm. This supports Nichols' (1972, p. 536) assumption that the tube feet of eleutherozoans, which are always single rather than arranged in triads, were derived from triadic tube feet of crinoid type. There was no previous clear evidence for this assumption, however, since in hemichordates, which are the closest living relatives of the dextiothetes, the ciliated outgrowths on each arm of the mesocoel (which are perhaps homologous to tube feet and function in producing a feeding current [Lester 1985]) are never arranged in triads.

The position of the radial water vessel in *D. scoticus* is uncertain. It presumably ran the length of the arm, giving rise to branches connected with the terminal water vessels. It may be represented by a dorsal ridge on the internal mould which follows the dorsal edge of the arm (text-fig. 11e; pl. 2, fig. 1, text-fig. 5), or it may have been more ventral than this, somewhere inside the arm. The obvious flexibility of the arm suggests that there would have been large longitudinal muscles in it in life, probably filling much of its volume.

Beneath the hydropore, immediately behind the oral partition, a small upwardly pointed projection is present on the internal mould (hydropore duct: pl. 2, figs. 2, 3, text-fig. 5; pl. 4, fig. 1, text-fig. 7; pl. 5, fig. 1, text-fig. 8). This presumably represents the dorsal end of the axial sinus which opens into the hydropore in echinoderms (Fedotov 1924). By analogy with extant echinoderms, the water vascular system would have joined the axial sinus inside the animal and would thus have been connected, indirectly, with the outside world. However, any such internal connection in *D. scoticus* does not show in the internal mould. The heart of *D. scoticus*, or in echinoderm terms the dorsal sac (= madreporic vesicle), would also probably have been situated near the hydropore, but its position cannot be identified in the fossils.

The position of the gonad, inside the anterior dorsal prominence of the head, has been suggested already. Its likely boundary on the internal mould is indicated by a slight groove which almost encircles the dorsal anterior prominence and passes at the left from the dorsal to the ventral surface (text-fig. 11; pl. 1, fig. 2, text-fig. 4; pl. 2, fig. 1, text-fig. 5; pl. 4, figs. 1, 3, 5, text-fig. 7). Corrugations on the surface of the internal mould (pl. 4, figs. 1, 3) run forwards from this groove, in some specimens, and suggest that the surface of the gonad was plicated in life. How the gonad terminated in a ventro-posterior direction is unclear: it may, in the largest individuals, have projected rearwards and downwards into the pharynx behind it (whose disposition will be explained below) so as to fill

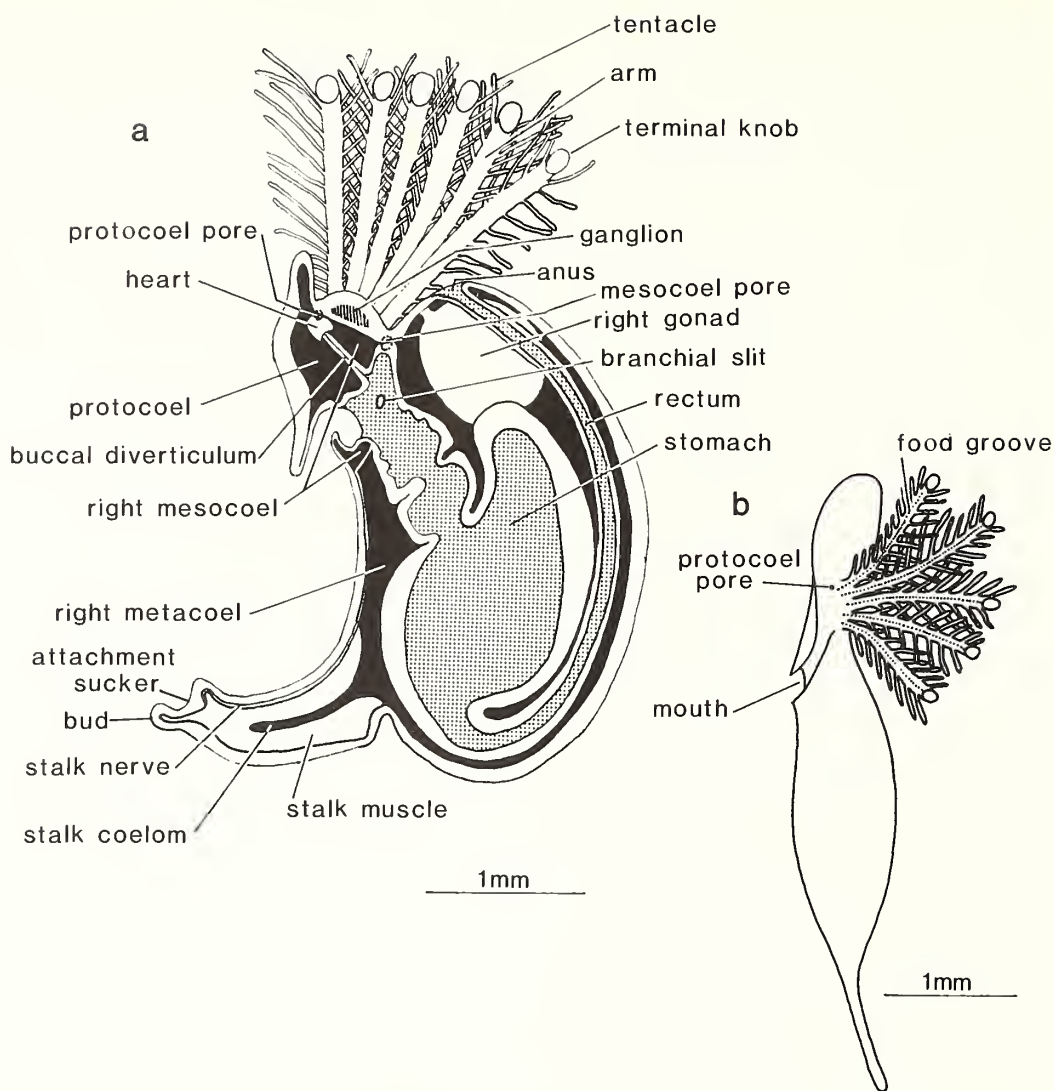
a large part of the ventral anterior prominence. Such a morphology would explain why this prominence is relatively large in the biggest of all observed individuals (pl. 1, fig. 1, text-fig. 4). On the other hand, it may be that the ventral anterior prominence corresponded to some other organ which expanded disproportionately in old age, perhaps part of the pharynx. It is clear, from the inferred position of the gonad in the internal mould, that the most anterior part of it, at least, was dorsal to the pharynx.

The pharynx would be expected to run, as in cornutes, from the gill slit at posterior left, to the velar mouth, and the buccal cavity would run from the velar mouth to the true mouth. The likely position of the pharynx in *D. scoticus*, or of the pharynx posteriorly and the buccal cavity anteriorly, is indicated by a sinuous tract with this oblique disposition, limited at anterior left and posterior right by grooves on the dorsal and ventral surfaces of the internal mould. There is no way of saying whether *D. scoticus* had a buccal cavity or, if it did have one, where the boundary between this cavity and the pharynx may have lain.

On the dorsal surface of the internal mould, the anterior limiting groove of the presumed pharynx *plus* buccal cavity coincided in its most anterior and rightmost part with the posterior limit of the probable gonad, as proposed above (pl. 1, fig. 2, text-fig. 4; pl. 4, fig. 5, text-fig. 7). More leftward, the anterior dorsal pharyngeal groove departs from the groove bounding the gonad, and bends to pass leftward and posteriorly, parallel to the posterior left margin of the head (pl. 4, figs. 2, 5, text-fig. 7). Perhaps the groove in this region separated the pharynx from muscles which pulled the roof downwards about the left peripheral hinge line (already mentioned) and which thus squirted water through the gill slit. The groove bounding the pharynx *plus* buccal cavity to the right and behind on the dorsal surface (pl. 1, fig. 2, text-fig. 4; pl. 2, fig. 1, text-fig. 5; pl. 3, fig. 8, text-fig. 6; pl. 4, figs. 2, 5, text-fig. 7) has a sinuous course parallel to the left anterior pharyngeal groove. Its exact course gives the strong impression of being deflected by an inflated, approximately spherical organ occupying the posterior prominence, possibly the stomach. This interpretation is suggested by comparing *D. scoticus* in dorsal aspect with the recent hemichordate *Cephalodiscus* in left aspect (text-fig. 13), on the assumption, already several times presented (e.g. Jefferies 1986, pp. 50ff., 221ff., and herein below) that the Dexiothetica are descended from a *Cephalodiscus*-like ancestor which lay down on its right side. For the stomach is the largest organ in the viscera in the trunk region of *Cephalodiscus* and, like the organ filling the posterior prominence of *D. scoticus*, is situated behind the pharynx and obliquely right of it in chordate terms (behind and dorsal to it in hemichordate terms). The posterior boundary of the stomach on the dorsal surface of the internal mould may be indicated by two grooves, approximately concentric to the highest point of the posterior dorsal prominence (pl. 2, fig. 1, text-fig. 5; pl. 3, fig. 8, text-fig. 6; pl. 4, figs. 2, 4, 6, text-fig. 7; pl. 5, fig. 1, text-fig. 8). One of these grooves runs leftward and forward from the left anterior margin of the likely position of the brain, while the other one runs rightwards and forwards from the right anterior part of the brain. The rest of the non-pharyngeal gut, probably an intestine ending in a rectum, presumably ran from the stomach to the anus but there is no indication of it in the internal moulds.

On the ventral surface of the internal mould (pl. 1, fig. 1, text-fig. 4), the likely position of the pharynx *plus* buccal cavity is, once again, indicated by two weak sinuous grooves. The more posterior of these, limiting the presumed pharynx posteriorly, runs around the front of the suggested position of the stomach and then passes leftward and rearward to the region of the gill slit ('left' and 'right' here refer always to the animal, not to the reader). The groove bounding the pharynx left anteriorly is very weak in its anterior part, but becomes stronger as it approaches the left border of the head, and then turns to run leftward and posteriorly parallel to that border. Perhaps this groove represents the right edge of muscles associated with the left hinge line. A somewhat similar weak groove runs parallel to the right border of the head and possibly delimits muscle which could lower the roof of the head on the right – as already explained, the elongate shape of the periproctal plates, especially left of the anus, suggests, although there was no right hinge line, that the right part of the head roof could be depressed, presumably by the action of muscles beneath it.

The distinction between buccal cavity and pharynx, as already implied, is uncertain in *D. scoticus*. In embryological terms, this distinction ought to coincide with that between endoderm and



TEXT-FIG. 13. *Cephalodiscus* after Schepotieff (1907) and Andersson (1907); (a) sagittal section with the organs of the right side; (b) external features.

ectoderm. It is fairly certain that the epithelium lining the food groove of *D. scoticus* would be ectodermal, on echinoderm analogies, and also almost certain that the gill slit would emerge from endoderm, and therefore from pharynx. Moreover, in cornutes the distinction between buccal cavity and pharynx can usually be plausibly recognised (e.g. Jefferies 1986, in *Cothurnocystis* p. 198; *Scotiaecystis* p. 211; *Ceratocystis* p. 217; *Nevadaecystis* p. 227; *Reticulocarpos* p. 225; *Galliaecystis* p. 235) and the same is sometimes true in mitrates (Jefferies 1986, *Placocystites* p. 269; *Lagynocystis* p. 295). In *D. scoticus*, however, there is no such visible distinction in the internal moulds. At one extreme, it seems possible that the mouth identified above was, in fact, the velar mouth, all gut inside it being endodermal. At the other extreme, it may be that the velar mouth was situated some distance internal to the identified mouth, but has left no trace on the internal moulds. The difficulty

is compounded by ambiguities in the hemichordate situation, for Lester (1988, p. 116) has recorded that the region usually called pharynx in *Rhabdopleura* is ectodermal in origin. It would be interesting to know whether the same is true in *Cephalodiscus* where, unlike *Rhabdopleura*, the walls of the 'pharynx' are penetrated by gill slits.

As for the brain of *D. scoticus*, on cornute and mitrate analogies this would be expected to lie at the anterior end of the tail. (In mitrates the identification of the brain as being located here is confirmed by detailed anatomical resemblances with the brain of fishes.) The internal moulds of plates M_{LD} and M_{RD} dorsally and of M_{PV} ventrally in *D. scoticus* carry strong grooves which seem to delimit the anterior border of the brain (pl. 1, figs. 10, 11; pl. 2, fig. 1, text-fig. 5; pl. 4, figs. 2, 4, text-fig. 7; pl. 5, fig. 1, text-fig. 8). These moulds suggest that the brain would be an approximately hemispherical structure which made contact with the skeleton on the inside of these plates. It would be directly comparable, in these respects, with the brain of the most anticrownward cornute *Ceratocystis perneri*.

The actual anterior border of the brain on the internal moulds, if it has not been exposed by dissection, appears asymmetrical, on the right projecting farther forward than on the left. Dissection of the internal moulds reveals, however, that this asymmetry is largely illusory, at least ventrally (pl. 1, figs. 10, 11) and is due to the way in which an approximately symmetrical brain intersects the asymmetrical surface of the posterior part of the internal mould of the head. The presumed brain does not occupy the whole extent of the tail insertion, being confined to the central part of the latter. Thus the natural mould of the tail insertion is strongly bipartite in appearance. In this way it resembles the tail insertion of mitrates which, in natural moulds, shows a positive replica of the bipartite brain, the two portions there corresponding to prosencephalon and deuterencephalon (Jefferies 1986, Chap. 8). It is unlikely, however, that the bipartition of the tail insertion has this meaning in *D. scoticus* for three reasons: (1) in mitrates and cornutes the stereom in contact with the nervous tissue is characteristically smooth whereas, in *D. scoticus*, only the central anterior portion of the tail insertion has a similar smoothness; (2) the left pyriform body of *D. scoticus* (no right one, if it existed, has been observed) seems to emerge medially just anterior to the presumed brain (text-fig. 11; pl. 1, figs. 9, 12, 13) and the pyriform body, being the trigeminal ganglion, would be related to nerves coming from the deuterencephalon, not from the prosencephalon; and (3) as shown by Cripps (1989b) the highly visible bipartition of the mitrate brain seems to have been evolved in the crownward parts of the chordate stem lineage since it is incipient in crownward cornutes and is not developed in anticrownward cornutes such as *Ceratocystis*.

The features of the internal mould of the tail have been discussed already. They are simple, however, and can conveniently be repeated here. In the hind tail of the fossils, there is a strand of rock, circular in cross section, corresponding to a canal in the skeleton, and situated dorsal to the centre of the hind tail in transverse section. This strand expands forwards conically in the mid-tail region, to join the approximately cylindrical infilling of the fore tail. As previously suggested, the infilling of the fore tail probably represents the position of muscles, presumably segmentally divided like the skeleton, and of a notochord. The muscles of the fore tail would end posteriorly by insertion into the conical skeleton of the mid tail. The notochord would continue rearwards into the hind tail and would correspond in position and shape to the central canal of the hind tail i.e. to the longitudinal strand of rock preserved in this region in the fossils between upper and lower hind-tail plates. I have argued elsewhere (Jefferies 1986, p. 202) that the notochord of cornutes and mitrates probably had a blood vessel along its central axis. The same conclusion applies to the presumed notochord in the hind tail of *D. scoticus*, since some blood supply to the posterior end of the hind tail would be needed and it could only have been delivered along the central canal between dorsal and ventral series of plates.

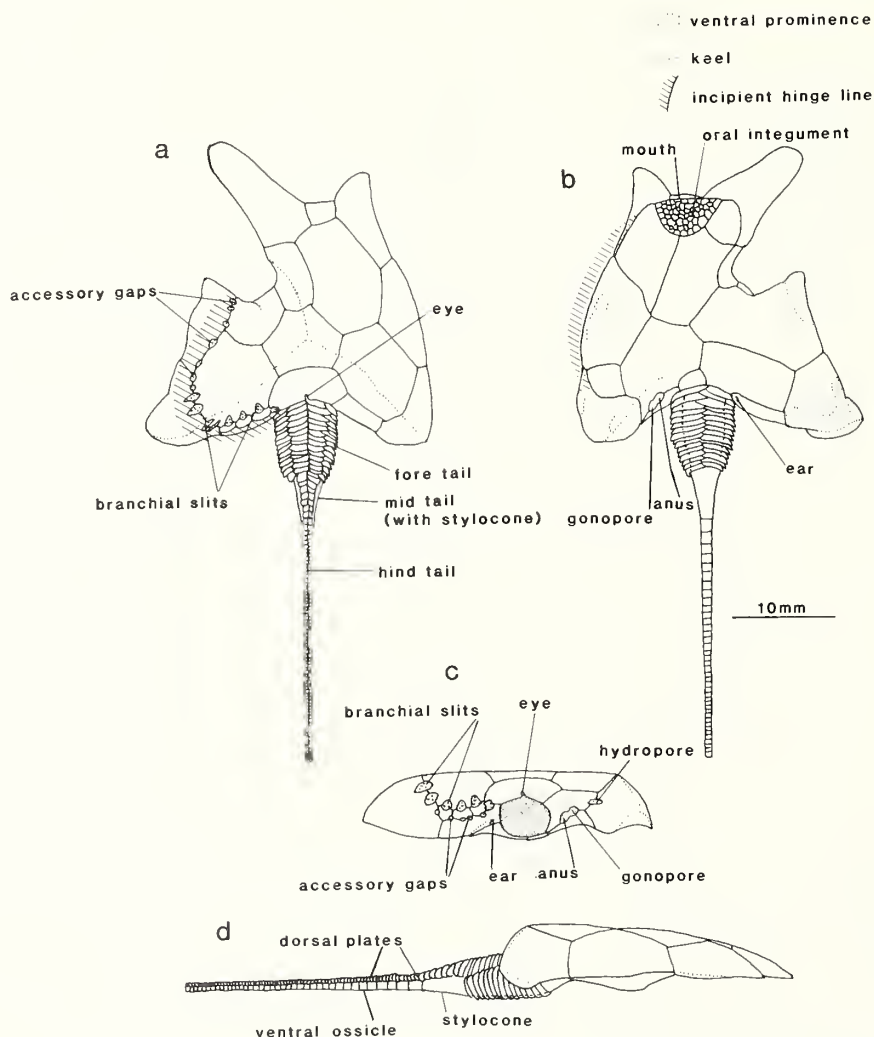
The pyriform body of *D. scoticus* has already been mentioned. It has been observed only on the left side of the brain and only in two specimens. One of these (pl. 1, figs. 12, 13) reveals it plainly in dorsal aspect inside plate M_{2LD} and the other, less clearly, in ventral aspect (pl. 1, fig. 9) inside plate M_{LV} . I have argued elsewhere that the left and right pyriform bodies of cornutes and mitrates are homologous respectively with the left and right trigeminal ganglia of vertebrates (Jefferies 1986,

p. 252, etc.) and the same would be true of this left pyriform body in a solute. It could easily be that a pyriform body existed also on the right in *D. scoticus* but has not been observed because it was never coated with calcite in life, i.e. it was never in contact with the nearest plates – in most specimens of *D. scoticus* the left pyriform body is as invisible as the possible right one.

ANATOMICAL COMPARISONS

Comparison of Dendrocystoides scoticus with cornutes

Ceratocystis perneri (text-fig. 14) is the only species of cornute known to have a hydropore (Jefferies 1969; 1986, p. 213ff). For this reason it is assigned to the least crownward plesion of the cornutes and is therefore the most suitable species for comparison with *D. scoticus*. (In the species *Ceratocystis vizainoi*, described by Ubahgs [1987], a hydropore may perhaps exist but has not been observed.)



TEXT-FIG. 14. *Ceratocystis perneri*, external anatomy, to show especially the tail, the head openings and the hinge lines at right and left of the head; (a) dorsal aspect; (b) ventral; (c) posterior; (d) right lateral.

D. scoticus resembles *Ceratocystis perneri* in the following respects: (1) it is divided into a head and a tail; (2) the ventral surface of the head is flatter than the dorsal surface; (3) the mouth is at anterior right of the head; (4) the anus is at right of the tail on the posterior surface of the head; (5) the gonopore and hydropore are right of the mid line and the gonopore is farther from the mouth than is the hydropore (against this, the hydropore and gonopore are anterior in position in *D. scoticus*, while the hydropore, if considered with respect to the centre of the head, is clockwise of the gonopore in *D. scoticus*, but anticlockwise of it in *C. perneri*); (6) there was an opening of the pharynx at posterior left of the head (in *D. scoticus* this seems to have been a single branchial opening or gill slit, whereas in *C. perneri* there are regularly seven gill slits); (7) the pharynx runs from anterior right towards the posterior left angle of the head – the extent of the buccal cavity, if there was one, is unknown in *D. scoticus*; (8) the non-pharyngeal gut would have lain posterior to, and right of, the pharynx, as indicated by the position of the anus in *D. scoticus*; (9) there was a brain at the tail insertion with a pyriform body (so far as observed on the left only in *D. scoticus*, but left and right of the brain in *C. perneri*); (10) there are indications that the roof of the head could be lowered in life – in *D. scoticus* these indications are the seeming hinge line on the left of the head and the horizontal elongation of the periproctal plates, while in *C. perneri* (Jefferies *et al.* 1987, p. 443) they are a probable hinge line on the right side of the head and accessory gaps, probably filled with muscle, on the left side of the head (text-fig. 14); (11) the tail is divided into fore, mid and hind regions; (12) the more massive skeletal elements of the hind tail are ventral, while the less massive are dorsal; (13) the skeleton of the fore tail is quadriserial and surrounds a large lumen, and the fore tail seems to be adapted to wave the mid and hind tail mainly from side to side. These resemblances are enough to show that *Dendrocystoides scoticus* can be regarded as built on the same basic plan as *Ceratocystis perneri* and other cornutes in general.

Moreover, the distal part of the hind tail was probably permanently and rigidly curved ventralwards in *D. scoticus*. Similarly, the distal part of the hind tail was able to curve ventrally in the cornute *Cothurnocystis elizae* (Jefferies 1986, p. 202). The same was probably true of the cornute *Protocystites* (Jefferies *et al.* 1987, p. 470). (Concerning *C. perneri* there is no evidence.) Both in primitive cornutes and in solutes, the downturned end of the hind tail probably served to grip the sea bottom during locomotion. It was probably used much like a punt pole in pulling the head rearwards.

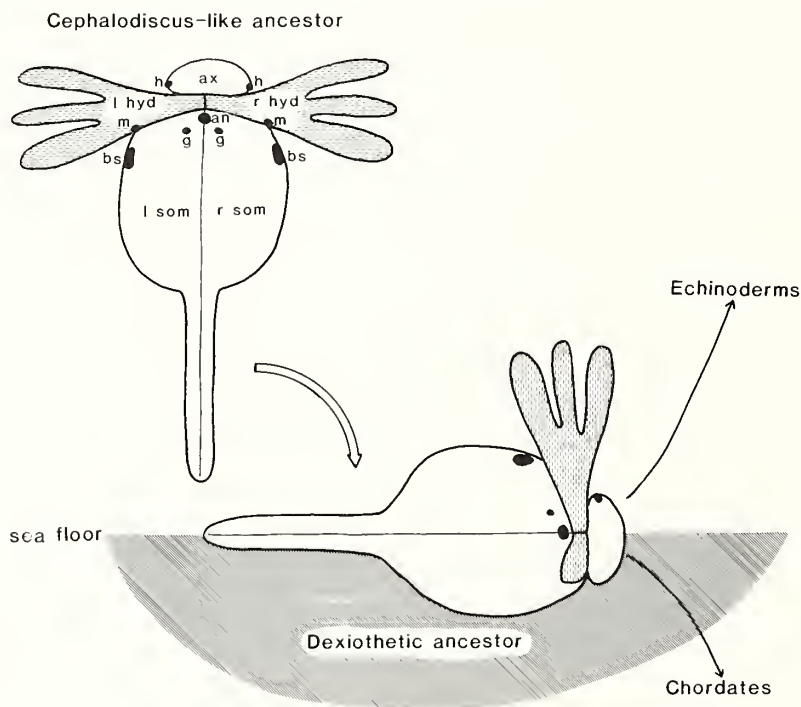
However, there are obvious differences between *Dendrocystoides scoticus* and cornutes, especially *Ceratocystis perneri*. These have partly been mentioned already, but for clarity I here list them all, even when this involves repetition: (1) *D. scoticus*, like all other solutes, had a feeding arm which seems to have been constructed on a standard echinoderm pattern with cover plates and triadic groups of tube feet – there is no such arm in the cornutes; (2) *D. scoticus* had an antibranchial process which is not represented in any cornute (though it is also absent in nearly all other solutes); (3) there was an anterior prominence, probably containing a gonad, near the anterior end of the head in *D. scoticus* – there was no such prominence in any cornute and the gonad in all cornutes was probably situated near the posterior right corner of the head; (4) the hydropores, on the hydropore node, were anterior in position and just right of and behind the mouth in *D. scoticus* where they penetrated the skeleton to form a madreporic plate – in cornutes the hydropore is only known to exist in *C. perneri* where it is slit-shaped and situated near the posterior right of the head; (5) the gonopores in *D. scoticus* are anterior, just left of the mouth, multiple and sometimes occluded – in *C. perneri*, which probably represents the primitive condition for cornutes, it is a single circular hole across a suture, is never occluded and is situated posteriorly in the head, just right of the anus; (6) *D. scoticus* had presumably only one gill slit (unless the gill slits were internal and the external branchial opening was an atrial opening) whereas *C. perneri* had seven such slits and other cornutes, except the most crownward ones where the number is irregular, had more than seven; (7) the head skeleton of *D. scoticus* consisted of a large number of plates, mostly irregular, whereas that of *C. perneri* was constructed of a smaller number of regular plates (none of the plates can reliably be homologized between the two species); (8) the brain of *D. scoticus* did not occupy the whole of the tail insertion, had no auditory groove or median eye, and was linked, so far as known, to a single pyriform body

(trigeminal ganglion) on the left, whereas the brain of *C. perneri* occupied the whole tail insertion, was associated with a pair of pyriform bodies and with an auditory groove and a median eye; (9) as to head chambers, there is no sign of a posterior coelom (left epicardium) in *D. scoticus*, whereas such seems to have existed in *C. perneri* and probably in all other cornutes; also it is uncertain whether or not *D. scoticus* had a buccal cavity; (10) the alternation of fore-tail plates on right and left is more irregular in *D. scoticus* than in *C. perneri* and the ventral overlap of right and left ventral plates is less extensive; (11) the mid-tail region of *D. scoticus* is altogether more irregular than that of *C. perneri* or any other cornute—in particular in *D. scoticus* there is no massive ossicle corresponding to the stylocone, while in cornutes nothing corresponds to the serial continuity of hind-tail plates with the right dorsal and right ventral plates of the fore tail in *D. scoticus*; (12) the hind tail of *D. scoticus* was rigid and its dorsal skeleton was constructed of a single unpaired series of rather long approximately hemicylindrical plates, not the right and left series of short imbricating plates seen in *C. perneri* and other cornutes.

The phylogenetic meaning of these differences from cornutes will be discussed below. Here I shall only repeat that, despite some differences, the fundamental identity of plan between solutes and cornutes seems obvious.

Comparison of Dendrocystoides scoticus with Cephalodiscus

The latest common ancestor of echinoderms and chordates, in my opinion, resembled the recent hemichordate *Cephalodiscus* but had become dexiothetic, i.e. had been modified to lie on its right side (Jefferies 1969, 1979, 1986, Chaps. 2 and 9; text-fig. 15 herein). In this respect, a comparison



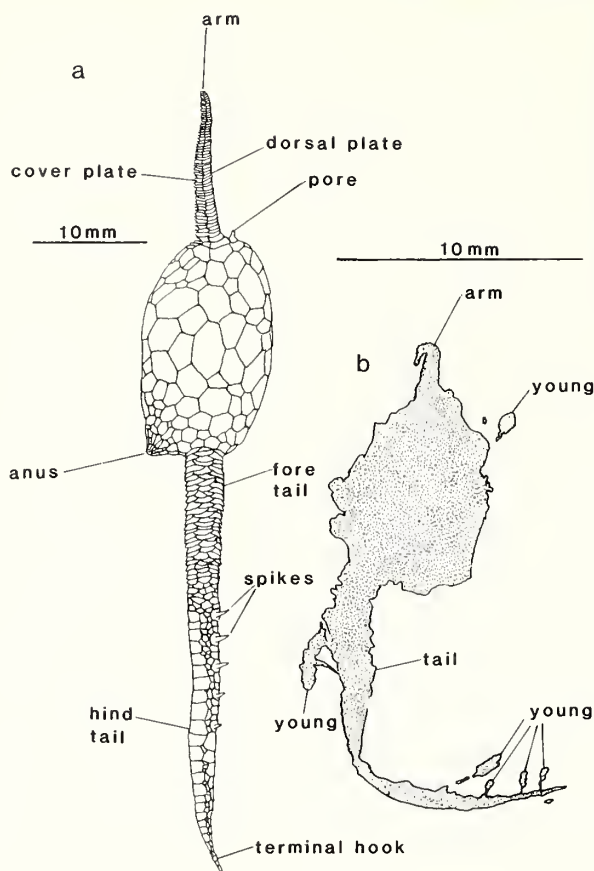
TEXT-FIG. 15. The dexiothetic rotation. In the origin of the Dexiothetica, it is likely that a *Cephalodiscus*-like ancestor fell right-side downwards onto the mud of the sea floor and lost the openings and arms of the primitive right side in consequence. The stalk was retained and became the chordate tail; an = anus; ax = axocoel (protocoel); bs = branchial slit; g = gonopore; h = hydropore (left and right mesocoel pores); l. hyd, r. hyd = left and right hydrocoels (mesocoels); l. som, r. som = left and right somatocoels (metacoels).

between *Dendrocystoides scoticus* and *Cephalodiscus* is illuminating. I discuss the tail first, and then the head, beginning at the front and working rearwards.

An evolutionary change of orientation, such as dexiothetism, brings great danger of muddle in the description. I find it necessary to use two equivalent sets of terms. Thus, with reference to *Cephalodiscus*, I write of hemichordate-ventral, hemichordate-dorsal, etc., and with reference to *D. scoticus* I write of chordate-ventral, etc. The reader will understand this most easily by remembering that: hemichordate-left = chordate-dorsal; hemichordate-right = chordate-ventral; hemichordate-dorsal = chordate-right; hemichordate-ventral = chordate-left. Posterior and anterior mean approximately the same in hemichordates and chordates. In using these terms, I do not imply that *D. scoticus* was a chordate, though this was probably true as discussed later. I merely intend to assert that, for example, the dorsal surface of *D. scoticus* was homologous with the dorsal surface of Man. The hemichordate terminology for orientation is the same as that traditionally used in describing echinoderm larvae.

The tail is the first noteworthy point of comparison. *D. scoticus*, like all other solutes and also the cornutes and mitrates, was divided into a tail and a head. In like manner, *Cephalodiscus* is divided into a stalk and the rest of the body. This stalk can be markedly lengthened or shortened and is used, in prehensile fashion, in collaboration with the head shield, for climbing up and down a horny skeletal process which projects upwards from the coenoecial cup. (In the tubeless hemichordate *Atubaria* the stalk is similarly used for clambering over hydroids [Sato 1936].) It is likely that the tail of *D. scoticus* was likewise locomotory, serving to pull the head rearwards over the sea floor like the tail of cornutes and mitrates, probably by side-to-side motion as in primitive cornutes. The stalk of *Cephalodiscus* would differ from the tail of *D. scoticus* in its mode of action, however, since the latter could bend proximally but was probably in all parts constant in length – this constancy of length certainly held for the rigid mid- and hind-tail regions but, in addition, the plates of the fore tail, because of their dorsal and ventral overlaps and sutures at right and left, suggest that the fore tail could bend right and left but not shorten or lengthen. This in turn suggests that the fore tail contained an incompressible but flexible notochord, as was probably true in cornutes and mitrates also. The notochord probably continued rearwards from the fore tail of *D. scoticus* to fill the canal between the dorsal and ventral plates of the hind tail, just as the notochord of the cornutes probably continued posteriorly into the median groove of the ventral hind-tail ossicles. There is no notochord in the stalk of *Cephalodiscus*, and its very absence allows the stalk to stretch and shorten.

An attachment sucker exists at the distal end of the stalk of *Cephalodiscus* (text-fig. 13). By means of this sucker, the animal fixes itself, at will, to the surface of the horny coenoecium – usually to the inner face of the coenoecial cup. There is no sign of such a sucker on the end of the tail of *D. scoticus*, though this may be due to ignorance, since the end of the tail has seldom been seen. It is fascinating to note, however, that Ubaghs (*in* Ubaghs and Robison 1985) observed in the Middle Cambrian solute *Castericystis vali* Ubaghs and Robison 1985 (text-fig. 16) that the adults often carry on their surface small, and therefore presumably young, individuals of the same species. These small animals are attached to the adult by distal ends of their tails. This strongly suggests that, at least in juveniles, the tail of *G. vali* had an attachment sucker at its distal end, perhaps followed in time by temporary cementation. (An alternative hypothesis, that the juveniles arose by budding from the associated adult, is unlikely because the juveniles are disposed seemingly at random on the adult body, whether on the head or the tail, with no orderly relationship between the size of the juvenile and its position on the adult.) If the tail of *C. vali* had a sucker on its end in the juvenile, a comparison with the stalk of *Cephalodiscus* is reinforced. I therefore propose that the stalk of hemichordates is homologous with the tail of solutes, and also with the tail of chordates in general. I first implied that the stalk of *Cephalodiscus* was homologous with the tail of cornutes (then called by me the stem) in Jefferies (1969). Gradually I abandoned this view for lack of evidence and in my book of 1986 I did not even mention it as a possibility. Ubaghs' interesting observations now make it likely again. I therefore now agree with the percipient remark of Eaton (1970, p. 977) when he said that: '...it is highly probable that the tail [of cornutes and mitrates] is a specialized version of the pterobranch peduncle.' Henceforth I shall stress this presumed homology by referring to the stalk of



TEXT-FIG. 16. *Castericystis vali* Ubaghs and Robison 1985 – a solute from the Middle Cambrian Marjum Formation of Utah (USA). (a) Reconstruction redrawn after fig. 1 of Ubaghs and Robison (1985) – the reconstruction is in an anatomically possible position for a corpse, but the hind tail is in right aspect, the head in ventral aspect and the arm in left aspect; (b) drawing traced from a photograph (Ubaghs and Robison 1985, fig. 11/5) to show the presence of young individuals of the species fixed to a presumed adult by the ends of their tails ($\times 3.5$).

hemichordates as the tail. In this I follow the usage of Burdon-Jones (1952) when he described the homologous organ of post-larval enteropneusts.

The planes of bilateral symmetry in the tails of *D. scoticus* and *Cephalodiscus* do not correspond to each other, if *D. scoticus* is supposed to have undergone a dexiothetic rotation: in *Cephalodiscus* the plane of symmetry in the tail is sagittal, which ought to correspond to chordate-horizontal, but the plane of symmetry in the tail of *D. scoticus*, admittedly imperfect in the mid and fore tail, is vertical. The position of the plane of symmetry has therefore rotated through 90° , either clockwise or anticlockwise when seen from behind, from hemichordate-sagittal to chordate-sagittal, thus counteracting the dexiothetic rotation.

The feeding arm of *D. scoticus*, with its ventrally-opening cover plates and its presumed ambulacral groove, water vascular canal and tube feet in probable triads, projects from the head at the opposite pole to the tail. The obviously comparable structure in *Cephalodiscus* would be part of the arm apparatus. More exactly, the best comparison would be with a single arm of the left side of *Cephalodiscus*. For the feeding arm of *D. scoticus* is presumably homologous with part of the water vascular system of echinoderms, and this system, in turn, is homologous with the left arm apparatus (left mesocoel = left hydrocoel) of *Cephalodiscus* (Jefferies 1986, p. 318).

There are difficulties in this comparison, however. For in a *Cephalodiscus* seen from the left side, the left arms present their food grooves toward the observer, whereas the food groove of *D. scoticus* in dorsal aspect faced away from the observer. If *Cephalodiscus* represents the primitive condition, therefore, the feeding arm of *D. scoticus* has rotated through 180° so that the food groove opens not towards chordate-dorsal but towards chordate-ventral. The right and left mesocoels of

Cephalodiscus open to the outside each by a mesocoel pore. In common with echinoderms, *D. scoticus* had no trace of any such pore so perhaps, as in echinoderms, the left mesocoel communicated with the axocoel (= protocoel) by a stone canal while the right mesocoel, together with its pore, had disappeared. Rehkämer and Welsch (1988) have stressed the fine-structural similarities between the stone canal of echinoderms and the mesocoel pores of *Cephalodiscus*. These resemblances suggest to me that perhaps the stone canal is homologous with the left mesocoel pore of hemichordates but has come to open into the protocoel (= axocoel) instead of direct to the outside.

The mouth of *Cephalodiscus* opens, in a hemichordate-ventral position, behind the head shield and faces posteriorly, toward the tail. The mouth of *D. scoticus*, on the other hand, is anterior and at chordate-right. In passing from the *Cephalodiscus* condition to the *D. scoticus* condition, therefore, the mouth would have rotated through some 160°, clockwise in chordate-dorsal aspect, about a vertical axis. Such a rotation would shift the left protocoel pore (equivalent to the hydropore of *D. scoticus* and the echinoderms) from a position anterior to the mouth to one where it lay, as actually observed in *D. scoticus*, chordate-right of the mouth. This suggests that, in addition to the dexiothetic rotation, *D. scoticus* differs from *Cephalodiscus* in having undergone a clockwise rotation of the anterior part of the head about a chordate-vertical axis. I shall refer to this additional rotation as anteriorisation of the mouth. The same rotation would perhaps explain another difference between *Cephalodiscus* and *D. scoticus*, namely the absence from the latter of any externally distinguishable part of the body corresponding to the head shield (protosome). Presumably, *D. scoticus* had an equivalent of the protosome, in that it would have possessed a protocoel (axocoel) buried inside the head and opening upwards at the hydropore. The burial of the protosome in the head might easily result from anteriorization of the mouth since the mouth, in moving chordate-rightwards and anteriorly, would press on the protosome. Such burial of the protosome is presumably a derived feature which *D. scoticus* shared with echinoderms and also with definite chordates, since the cornute *Ceratocystis* had a hydropore but no externally distinct protosomal body region. The heart and pericardium of *D. scoticus* would probably be near the hydropore, like the equivalent head process of the axial organ and dorsal sac of echinoderms. These structures are equivalent to the heart and pericardium in the protocoel of hemichordates, which lie anterior to the mouth in *Cephalodiscus*. The rotation involved in anteriorizing the mouth of *C. scoticus* would have shifted the heart and pericardium to their presumed new positions also.

As for the gonad, I have argued above that the anterior prominence of *D. scoticus* contained a gonad which issued by a group of gonopores at the chordate-anterior-right of the prominence. The gonad, being chordate-dorsal in position, presumably corresponds to the left gonad of *Cephalodiscus* and the gonopores to the left gonopore. In general position at the anterior end of the body farthest from the tail, the gonad of *D. scoticus* is comparable with the left gonad of *Cephalodiscus* and contrasts in both these animals with the cornute situation where the gonad was at chordate-right and posterior in the head. However, there are also differences between *Cephalodiscus* and *D. scoticus* since in the latter the gonad and gonopore lay chordate-left of the arm whereas in *Cephalodiscus* they were at chordate-right of the arms (dorsal to them in hemichordate terms). In passing from *Cephalodiscus* to *D. scoticus*, therefore, the gonopore and gonad would move chordate-leftwards. I cannot decide whether this was part of the clockwise rotation of the anterior part of the head implied by the anteriorization of the mouth, or whether it was an independent process.

The embryological origin of the gonad of echinoderms is interesting here: the primordial germ cells are said to arise from the wall of the left somatocoel in crinoids (MacBride 1914, p. 552), in asteroids (Gemmill 1914) in crinoids (Hyman 1955, p. 502) and in ophiuroids (Hyman 1955, p. 636). (No comparable statement can be made for the holothuroids, perhaps because the distinction between left and right somatocoels breaks down at an early stage.) It seems likely, therefore, that the gonad or gonads of echinoderms, like that of *D. scoticus*, correspond to the left gonad of *Cephalodiscus*.

The pharynx of *D. scoticus* seems to have been elongate, stretching from the mouth or velar mouth at anterior chordate-right to the gill slit at posterior chordate-left, with presumably an

oesophageal opening posterior and right of it somewhere along its course. (A dubious point, as already mentioned, is whether *D. scoticus* had a buccal cavity.) The position of the pharynx in *D. scoticus* is broadly the same as in *Cephalodiscus* seen from the left, but the two pharynges differ in shape. The differences correspond to extension of the pharynx chordate-leftwards and rearwards and chordate-rightwards and forwards in *D. scoticus*, with the loss of a gill slit (the hemichordate right gill slit) and the migration of the remaining gill slit to a chordate-left-posterior position. In these respects, the pharynx of *D. scoticus* was more cornute-like than that of *Cephalodiscus*.

Concerning the non-pharyngeal gut, the stomach of *D. scoticus* probably coincided in position with the posterior dorsal and ventral prominences. This position, near the centre of the head, is comparable with the stomach of *Cephalodiscus* as seen from the left. The position of the anus in *Cephalodiscus* and *D. scoticus* is comparable in being, in both animals, chordate-right of the tail, but it differs in being more posterior in *D. scoticus*, nearer to the proximal end of the tail. This difference in the position of the anus implies that the intestine and rectum must also have been differently disposed, but nothing precise can be said about this since there is no evidence in *D. scoticus* of the course of the gut between stomach and anus.

Not much can be said about the positions of the coeloms in *D. scoticus*, compared with *Cephalodiscus*. If *D. scoticus* has undergone a dexiothetic rotation with respect to *Cephalodiscus*, then the right somatocoel (= right metacoel) would be downward and the left somatocoel upward, as is primitively the case in echinoderms (Jefferies 1986, p. 51) and as seems also to have been true in cornutes and mitrates (Jefferies 1986, p. 198ff. in discussing left and right anterior coeloms = left and right somatocoels). The mesentery between the two somatocoels would thus be horizontal. The left hydrocoel (= left mesocoel) would be located in the feeding arm while the right hydrocoel (= right mesocoel) would have disappeared. And the axocoel (= protoceol), buried inside the head but single and unpaired as in hemichordates, would open upwards at the hydropore, just right of the mouth and right of the arm base, the hemichordate right protoceol pore having disappeared.

Finally as for size, *D. scoticus*, like all other solutes, was about 30 mm in head length and therefore much bigger than *Cephalodiscus*, whose greatest head length is about 5 mm.

To summarize, if *D. scoticus* is compared with a *Cephalodiscus* lying on its right side, and if the latter is assumed, in all respects, to represent the primitive condition, then the following changes would have occurred in passing from *Cephalodiscus* to *D. scoticus*.

(1) The evolution of a calcite skeleton and the formation of specialized plates in some regions, especially in the tail, the tail insertion, the arm and the arm insertion.

(2) The evolution of a vertical plane of symmetry in the tail and probably the origin of the notochord so that locomotion took place by lateral bending of the tail, rather than by shortening and lengthening of it; loss of the power of budding, which had been located in *Cephalodiscus* at the distal end of the tail.

(3) Loss of all the hemichordate-right arm apparatus and all but one arm of the hemichordate-left arm apparatus; rotation of the remaining left arm through 180° so that the food groove opened chordate-downwards; development of a triadic arrangement of tube feet regularly related to the cover plates; loss of the hemichordate-left and hemichordate-right mesocoel pores. (Perhaps the hemichordate left mesocoel pore became the stone canal of dexiothetes, which in extant forms is retained in echinoderms but absent in chordates.)

(4) Anteriorization of the mouth, involving some degree of rotation of the anterior part of the body clockwise about a chordate-vertical axis, so that the hydropore came to lie chordate-right of the mouth rather than anterior to it; loss of the head shield (protosome) as an externally distinct body region, by burial of the protoceol (axocoel) in the body chordate-right of the mouth (this burial may have resulted from the anteriorization of the mouth, that is from the clockwise rotation of the anterior part of the head which such movement of the mouth implies); loss of the hemichordate-right, chordate-ventral protoceol pore; perhaps the evolution of a stone canal linking the hemichordate-left hydrocoel (= left mesocoel) with the axocoel (= protoceol).

(5) Loss of the hemichordate-right gonad and right gonopore; migration of the hemichordate-left

gonad and left gonopore chordate-leftwards, so as to lie left of the arm when *D. scoticus* is viewed in dorsal aspect.

(6) Movement of the hemichordate-left gill slit from a chordate-anterior-central to a chordate-left-posterior position, with corresponding elongation of the pharynx.

(7) Migration of the anus from chordate-anterior-right to chordate-posterior-right in the head.

(8) Evolution of a brain and a left trigeminal ganglion at the anterior end of the tail.

(9) Loss of the hemichordate-right hydrocoel (= right mesocoel); repositioning of the hemichordate-right and -left metacoels, as a result of dextiothetic rotation of the animal, to become respectively chordate-ventral and chordate-dorsal.

(10) Increase in size.

Not all these changes would actually have happened since *Cephalodiscus* is probably not in all ways more primitive than *D. scoticus*.

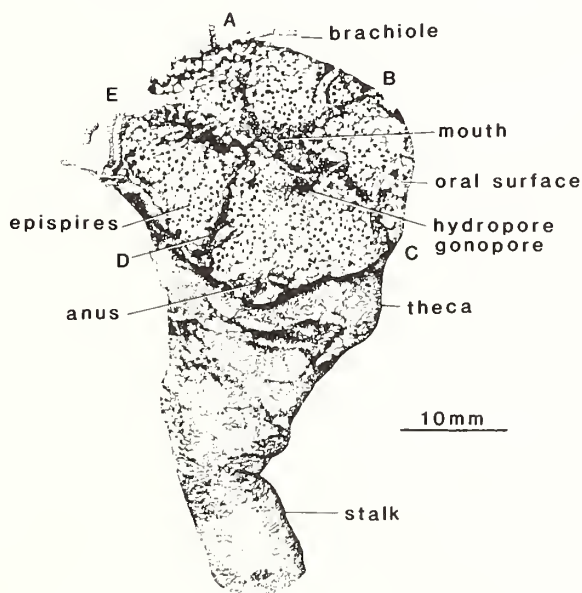
Comparison of Cephalodiscus with Kinzercystis

The 'eocrinoid' *Kinzercystis* (text-fig. 17), from the Lower Cambrian Kinzers Formation of Pennsylvania in the U.S.A., has been well described and reconstructed by Sprinkle (1973) and Paul and Smith (1984). The latter authors regard it as belonging to the crown group of the echinoderms, seeing it as a primitive member of the Pelmatozoa. I choose it for comparison here for three reasons: because it is well studied; because, unlike most primitive echinoderms, the hydropore is separate from the gonopore; and because I wish to simplify the phylogenetic argument by concentrating on one quinquerradiate echinoderm only.

Kinzercystis was a small animal about 30 mm in height and 25 mm in greatest width. It was an inverted truncated cone in shape and plated all over with calcite plates. The wide end of the cone, which would have faced upward in life, was the oral surface while the truncation of the cone, downward in life, was developed as a circular attachment area by which the animal could fix itself to objects on the sea floor.

The oral surface was approximately circular with an elongate mouth near the centre, roofed over by cover plates. Three ambulacral grooves radiate from the mouth, and two of these split into two not far from the mouth. This produces five food grooves in all, with a 2+1+2 arrangement suggesting a vestigial triradiality. The undivided food groove is conventionally labelled A and the

TEXT-FIG. 17. The eocrinoid *Kinzercystis durhami* Sprinkle 1973 from the Lower Cambrian Kinzers Formation of Pennsylvania (USA). Copied from Paul and Smith (1984, fig. 8) and relabelled.



others, in clockwise direction seen from above, are numbered B, C, D and E. Conventionally the A food groove is taken as anterior and the C–D interradius as posterior. In the C–D interradius, just behind and to the right of the mouth when seen from above, there are two openings very close to each other. The opening nearer to the mouth is spout-shaped and is identified by Paul and Smith as the hydropore while the other opening, guarded by a pyramid of small spike-shaped plates and therefore intermittently closable in life, is identified by them as the gonopore. (Sprinkle [1973, p. 74] labelled hydropore and gonopore conversely, but Paul and Smith's view is preferable because it agrees with the situation in cystoids and because it is reasonable to suppose that a gonopore could be closed intermittently.) Also in the C–D interradius, near the edge of the oral surface and left of the mouth as seen from above, was the anus guarded by an anal pyramid.

Each ambulacral groove rested on two series of flooring plates and was covered on each side by a plated lip – the plates of these lips are called cover plates. On either side of each ambulacral groove, alternating in position, was a series of flexible plated appendages called brachioles which Paul and Smith interpret, for good reasons, as plated tube feet. The interambulacra were covered with large plates which, at their sutures, carried openings called epispires. These may have had a respiratory function, each one marking the position of a thin-called external gill or papula.

The aboral surface of *Kinzercystis* was in two parts – the distal attachment area and the rest. The attachment area was approximately circular and plated with polygonal plates, whereas the remainder of the aboral surface, vaguely divided into an upper wider theca and a lower almost cylindrical holdfast, is covered with imbricating plates (Sprinkle, 1973, p.70, fig. 22). The imbrication is such that, seen from outside, lower plates overlap the lower parts of higher ones. This imbrication suggests that the aboral surface was able to elongate and shorten.

Kinzercystis can be interpreted, in its main anatomical features, by comparison with crinoids (for references see Jefferies 1986, pp. 47ff.). It is highly probable that, at least in the juvenile stages, a right and left somatocoel would have been present, with the right somatocoel located toward the attachment and the left somatocoel lying orally. Much of the gut would have been situated between the two somatocoels. The ambulacral grooves would have been occupied by radial water vessels with brachioles representing the tube feet, and this water vascular system would correspond to the left hydrocoel of the larva. The hydropore would be the opening of the axocoel and would communicate with the water vascular system by a stone canal. The attachment area would be homologous with the axocoel attachment area of the larva and thus with the ventral surface of the head shield of *Cephalodiscus*. The gonad, opening at the gonopore, would probably be homologous with the left gonad of *Cephalodiscus* as suggested above.

In comparing *Kinzercystis* with *Cephalodiscus* I shall assume, as when discussing *Dendrocystoides scoticus*, that *Cephalodiscus* in most ways represents the primitive condition. Some of the differences between *Cephalodiscus* and *Kinzercystis* are shared by the latter with *D. scoticus* and can be seen as synapomorphies of *D. scoticus* and *Kinzercystis* in a three-taxon comparison. Such include:

(1) The dexiothetic rotation, with the oral surface of *Kinzercystis* corresponding to the dorsal surface of *D. scoticus* and to the left side of *Cephalodiscus* – other results of dexiothetism include the absence of the hemichordate-right arm system and right mesocoel pore and of the hemichordate-right gill slit, gonad and gonopore.

(2) The calcitic skeleton.

(3) The disappearance of the protosome as an externally distinct body region, presumably by becoming buried in the body though still opening outwards by the hydropore.

(4) The disappearance of the right mesocoel pore, presumably because the water vascular system communicated with the protosome by a stone canal inside the body.

All four of these advanced resemblances between *Kinzercystis* and *D. scoticus* can be seen as autapomorphies of the Dexiothetica.

Some features which differentiate *Kinzercystis* from *Cephalodiscus* are not shared with *D. scoticus*. These include:

(1) The absence of a tail.

(2) Attachment by the middle of the aboral (chordate-ventral) surface to some external object.

(3) The position of the mouth at the centre of the oral surface.

(4) The recumbent position of the water vascular system on the surface of the body and its division into five branches with a distinct 2+1+2 arrangement.

(5) The absence of any gill slit.

All five of these distinguishing features of *Kinzercystis* in the three-taxon comparison can be seen as autapomorphies of the crown echinoderms, except for attachment by the aboral surface to an outside object which is perhaps an autapomorphy of the pelmatozoans.

THE SYSTEMATIC POSITION OF *DENDROCYSTOIDES*

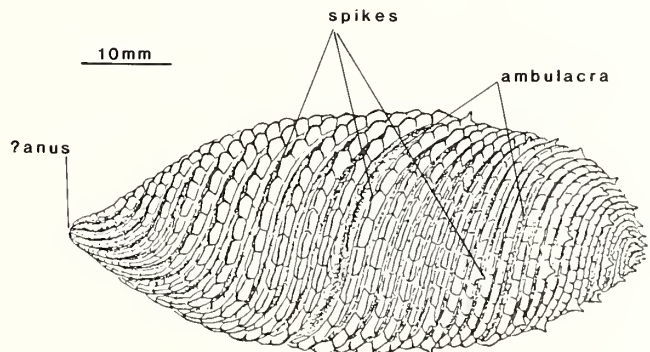
The analysis so far shows that *D. scoticus* was a member of the Dexiothetica, that it did not belong to the echinoderm crown group, nor to the chordate crown group, nor to the crownward members of the chordate stem group known as Cornuta. The methodology for placing it more exactly within the Dexiothetica is clear: if it lacked some autapomorphy of the Dexiothetica, it belongs in the stem group of that group; if it shared a synapomorphy with the chordates, particularly with the stem-group chordates of the Cornuta, it belongs in the chordate stem group; if it shared a synapomorphy with the echinoderms, it would belong in the stem group of the echinoderms; and if none of these conditions applied, it would have to remain in the nodal group of the Dexiothetica along with the latest common ancestor of chordates and echinoderms.

There are, in fact, many advanced features connecting *D. scoticus* with cornutes, which are not present in such a primitive echinoderm as *Kinzercystis* for example. In the tail these comprise: (1) the division into fore, mid and hind tail; (2) the quadriserial plating of the fore tail; and (3) the large lumen of the fore tail and its adaptation for bending from side to side, suggesting the presence of a notochord. Just anterior to the tail, *D. scoticus* shows advanced resemblances to cornutes, and to chordates in general, in having a brain and at least one pyriform body. Elsewhere in the head, advanced resemblances to cornutes include the position of the gill slit at posterior left and the corresponding leftward and posterior elongation of the pharynx.

Unfortunately, all these features relate either to the tail or to the gill slit, and both these organs are absent in echinoderms, probably having been lost. Loss of complex structures is intrinsically more likely than their origin. All these advanced resemblances are therefore dubious as synapomorphies between cornutes and *D. scoticus*, because of the possibility that the latest common ancestor of chordates and echinoderms may have had them but that they were then lost in the echinoderm stem lineage when the tail and the gill slit were lost.

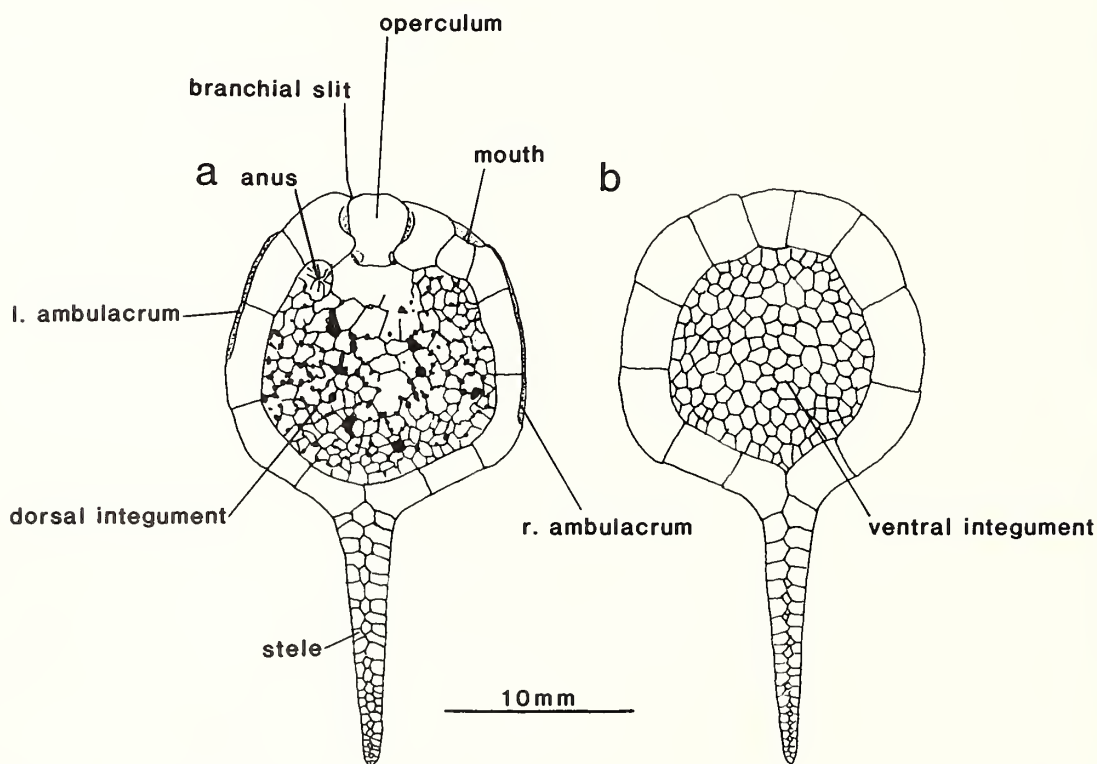
To eliminate this possibility, or perhaps to confirm it, will require study of the echinoderm stem group, to which, up till now, only one group of fossils has been assigned. These are the Helicoplacoidea (text-fig. 18) which Paul and Smith (1984) place as stem-group echinoderms on account of their triradial ambulacral system incorporated in the wall of the body, the mouth being, as Derstler (1981) suggested, at the junction of three ambulacral rays. The helicoplacoids, so far as

TEXT-FIG. 18. The helicoplacoid *Helicoplacus curtisi* Durham and Caster 1963. Reconstruction copied from Durham and Caster (1966, fig. 109a). The presence of spikes over the whole surface of the body suggests that the animal was totally buried in normal life, presumably with the long axis horizontal. About $\times 2$.



known, probably constitute a monophyletic group because of their strongly spiral skeleton. They have no gill slit or tail and these absences confirm their position as echinoderms. Unlike Paul and Smith, I believe that helicoplacoids probably lived entirely buried in the sea bottom, burrowing earthworm-fashion with the long axis horizontal, by dilating or extending different parts of the obviously flexible body. Their spiral structure suggests that they rotated about their long axis as they moved. My reason for suggesting that they lived entirely buried is the presence of low spikes on all parts of the external surface in *Helicoplacus curtisi* (text-fig. 18), *H. gilberti* (Durham and Caster 1966, fig. 107), *Waucobella nelsoni* (Durham 1967, pl. 14, fig. 5), and *Polyplacus kilmeri* (Durham 1967, pl. 14, fig. 1). These spikes look like sediment-gripping structures which could only have functioned when the whole surface of the animal made contact with mud. The helicoplacoids suggest that a triradiate ambulacral system recumbent on the body surface, rather than borne on arms, was evolved in the echinoderm stem lineage and that later this triradiate system gave rise to the quinquerradiate system with a 2+1+2 structure. An important conclusion is that the recumbency of the ambulacral system represents an autapomorphy of echinoderms, not shared by *Cephalodiscus* with its many arms nor by solutes with their single arm.

The Cincta may also belong to the echinoderm stem group. These fossils need restudy since Ubaghs' (1968) comprehensive treatment of them is now rather old. They can be exemplified by *Trochocystites* (text-fig. 19) which is shaped much like a tennis racquet with a theca and an appendage (stele). The animal lay with one face of the theca on the sea bottom and the other upwards. The theca is surrounded by a frame of marginal plates. The appendage or stele, at least proximally, would be stiff in a right-left direction, but perhaps able to bend up and down. In its plate arrangement it resembles an extension of the frame – the major series of plates, at right and



TEXT-FIG. 19. The cinctan *Trochocystites bohemicus* Barrande 1887. Reconstruction redrawn and modified from Ubaghs (1968, fig. 363): (a) dorsal aspect, to show anus at anterior left; (b) ventral aspect. $\times 2.5$.

left, resemble and pass into frame plates, whereas intercalated dorsal and ventral plates in the stele resemble dorsal and ventral integument plates in the theca, and probably represent serial homologues of these integument plates. Opposite the stele, two openings have so far been recorded in the literature. The opening more to the right, when the stele is towards the observer, had a pair of ambulacral grooves converging upon it, these grooves coming to it along the marginal frame from right and left. This opening was therefore the mouth which was thus at the centre of a biradial recumbent water vascular system. The two rays presumably correspond to the rays B/C and D/E of *Kinzercystis* and other quinquerradiata echinoderms. The other opening recorded in the literature was covered by a plate, the operculum, hinged at the top. This opening is conventionally interpreted as the anus. However, there is a third opening, not yet recorded in the literature, just to the left of the operculum (Prof. K. Sdzuy, personal communication). This third opening, which is visible in Ubaghs (1968, fig. 367/1), is guarded by a pyramid of plates and is likely to be the true anus. And, in that case, the operculate opening, which in its structure suggests an outlet valve, is probably a gill slit. The recumbency of the water vascular system of cinctans, if interpreted as a synapomorphy with the recumbent water vascular system of helicoplacoids, suggests that Cincta are stem-group echinoderms. This is confirmed by the biradiality of the water vascular system in Cincta, since the 2+1+2 pattern of water vascular system, can be construed as fundamentally biradial.

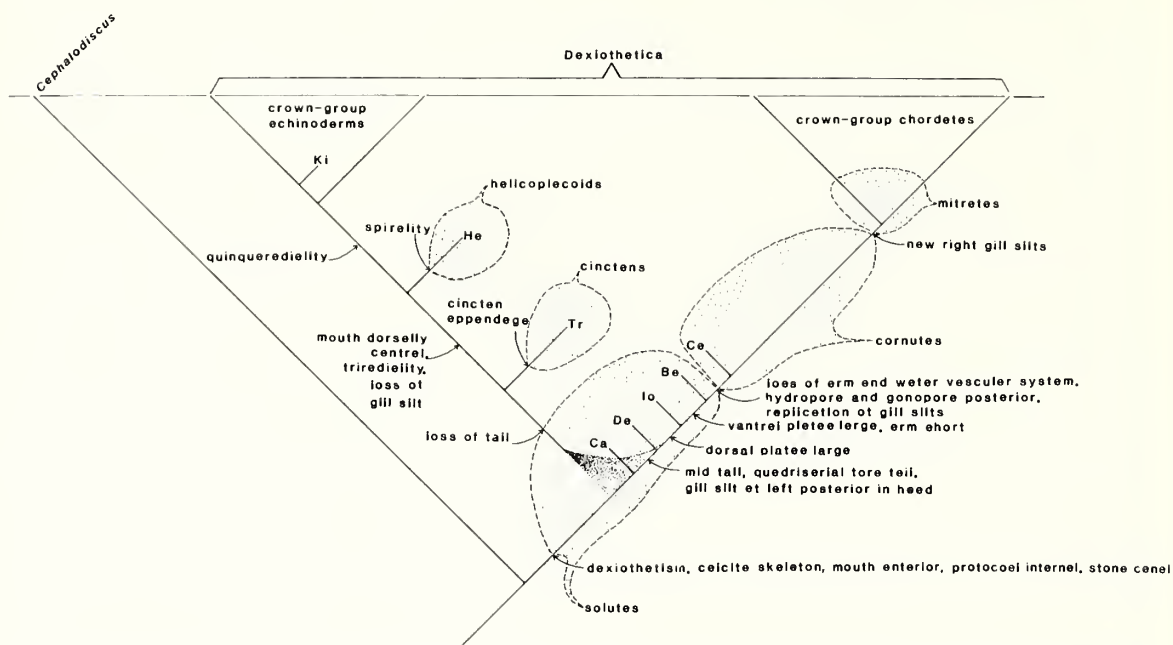
However, the Cincta are probably less crownward than helicoplacoids in the echinoderm stem group. This is for several reasons: (1) they retain a gill slit; (2) they have a biradial, rather than a triradial water vascular system; and (3) the mouth is in the hemichordate-sagittal plane, as in *Cephalodiscus* – not in the centre of the chordate-dorsal surface as in crown-group echinoderms and, probably, in helicoplacoids. The position of the gill slit, anterior in the body and near to the mouth, resembles that of the left gill slit in *Cephalodiscus* and is therefore probably primitive for echinoderms. This means that the gill slit of the latest common ancestor of chordates and echinoderms would also probably have been anterior in position. And in that case, the left posterior position of the gill slit of *D. scoticus* is probably a synapomorphy with cornutes. If so, then *D. scoticus* is a stem-group chordate, less crownward than any cornute.

The stele of Cincta is difficult to interpret and there are two main possibilities: (1) its position in the animal, as far as possible away from the mouth and therefore posterior, and the fact that it is biserial in its major plating, might suggest that it is homologous with the tail of hemichordates, solutes and chordates; but, (2) the fact that the two series of plates are at right and left, not as in solutes dorsal and ventral, and the fact that in some cinctans the two series are continuous with the marginal plates of the frame (e.g. *Trochocystites*, *Gyrocyctis*), might suggest that the stele arose within the Cincta, after the evolution of a marginal frame, as an extension of that frame, and that therefore it is not homologous with a tail. Further work is needed to establish which of these two alternatives is nearer the truth.

If the appendage of Cincta is genuinely a tail, then the chordate nature of *D. scoticus* is almost certain since the species would then share a large number of advanced tail features with the Cornuta which are absent in the Cincta. Such include: the brain; the left pyriform body; the fore, mid and hind regions of the tail; the large lumen of the fore tail, adapted for right-left bending and probably containing muscles and a notochord; and the ventral series of plates in the hind tail, corresponding to the ventral hind-tail ossicles of cornutes. At the moment, however, I am inclined to think that the stele of cincta is an autapomorphy of that group. If so, then the chordate nature of *D. scoticus* remains doubtful, based, as it is, on nothing but the posterior left position of the gill slit.

Whether or not *D. scoticus* is a chordate, it is almost certainly more closely related to the chordate crown group than is *Castericystis*. The conclusion is based on resemblances to *Ceratocystis* (a definite stem-group chordate) which *Castericystis* does not share: i.e., the distinctly tripartite tail of *D. scoticus*, with its stylocone-like mid tail and quadriserial fore tail. Moreover, some solutes resemble *Ceratocystis* still more closely. Thus *Iowacyctis* (Caster 1968, p. S620) has the fore tail sharply distinct from the rest of the tail and the dorsal surface of the head is formed of large plates, in both respects like *Ceratocystis*. And *Belemnocystites* is still more like *Ceratocystis* in having a big-

plated ventral (as well as dorsal) surface to the head and a very short arm (Caster 1968, p. S623) whereas cornutes have no arm at all. All this suggests that these four solutes are successively closer related to the chordate crown group in the sequence: *Castericystis*, *Dendrocystoides*, *Iowacystis*, *Belemnocystites*. I summarize the results of these arguments in a cladogram (text-fig. 20).



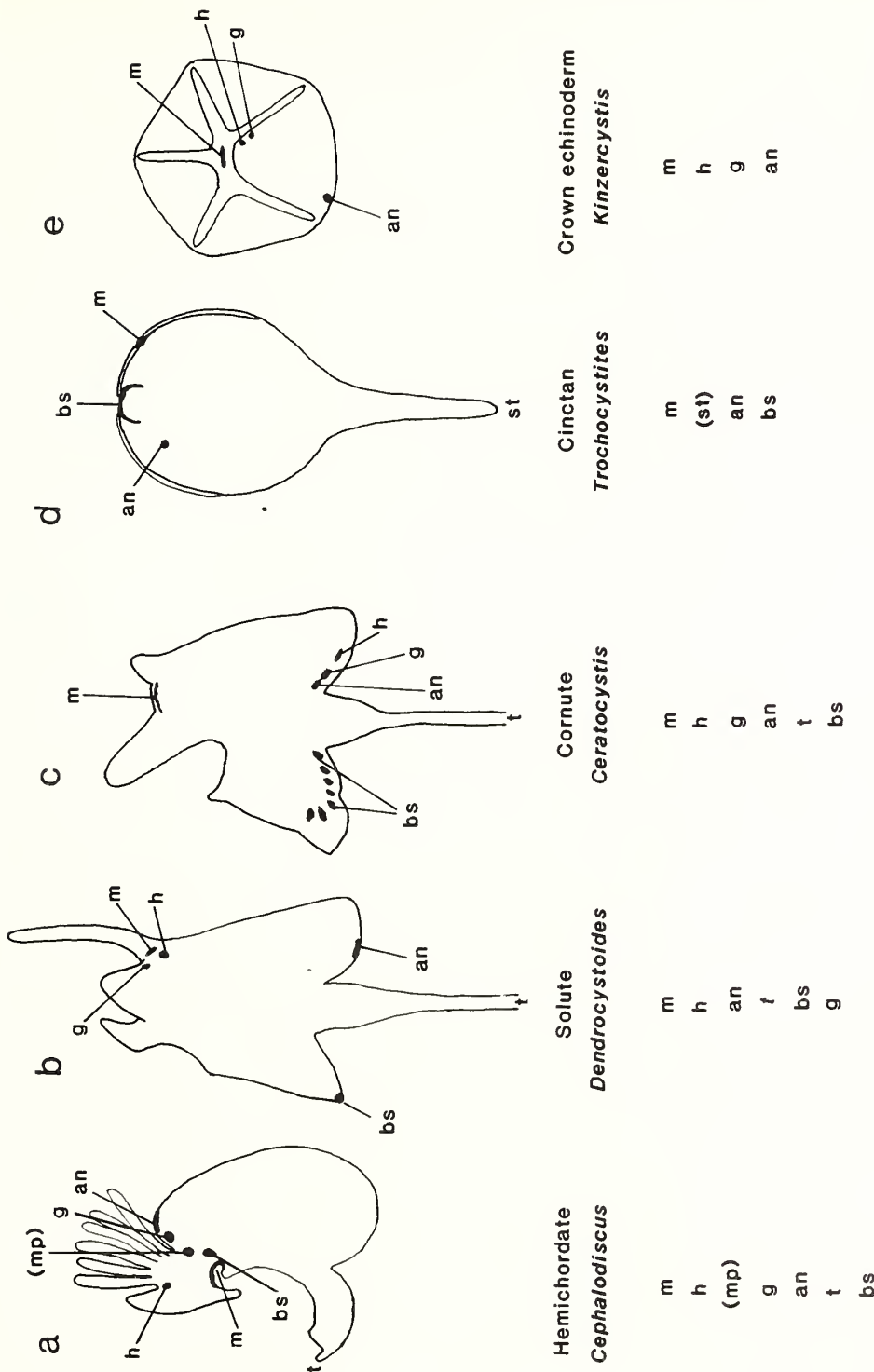
TEXT-FIG. 20. Cladogram of the deuterostomes, to show the phylogenetic position of the solutes within the Dextiothetica: Be = *Belemnocystites*; Ca = *Castericystis*; Ce = *Ceratocystis*; De = *Dendrocystoides*; He = *Helicoplacus*; Io = *Iowacystis*; Ki = *Kinzercystis*; Tr = *Trochocystites*.

As to the timing of the phylogenetic split between echinoderms and chordates, I formerly believed that this happened in the earliest Cambrian (Jefferies 1979, p. 475). This view was based on the assumption that the calcitic skeleton is homologous between echinoderms and chordates and on the further assumption that skeletons in general arose at the base of the Cambrian. The latter belief now seems to be mistaken, however, since Gehling (1987) has described an edrioasteroid-like fossil (*Arkarua adami*) from the late Precambrian Pound Quartzite of Australia. This form has a 2 + 1 + 2 symmetry and probably possessed a lightly built skeleton, since it seems to show a marginal ring of plates. If *Arkarua* is correctly regarded as a quinquerediate echinoderm, as seems likely, then the split between echinoderms and chordates must be older than it. Perhaps the separation occurred in the late Precambrian. This raises the interesting possibility that solutes will be found in the late Precambrian.

CONCLUSIONS

The main conclusions of this paper are as follows.

(1) *Dextiothetism*. Text-figure 21 summarizes the evidence for dextiothetism on the basis of the five animals particularly discussed above. In the diagrams all five are shown in chordate-dorsal aspect, meaning that *Cephalodiscus* is seen from the left while the other animals are seen from above. The view from above is called the dorsal aspect in *Dendrocystoides* and *Ceratocystis*, the upper surface in *Trochocystites* and the oral, or sometimes 'ventral' surface in quinquerediate echinoderms such as *Kinzercystis*.



TEXT-FIG. 21. The topological evidence for dextiothetism as shown by five deuterothetism in chordate-dorsal aspect, i.e. *Cephalodiscus* seen from the left and four dextiothetism seen from above. Tabulated below are the sequences of body openings and appendage passed in moving clockwise around each sketch, beginning at the mouth. m = mouth; h = hydropore (left protocol pore of *Cephalodiscus*; mp = mesocoel pore (of *Cephalodiscus* only); g = gonopore; an = anus; t = tail (stalk of *Cephalodiscus*); bs = branchial slit; st = cinctan stele.

A clockwise journey around each of the five sketches, beginning at the mouth, produces the tabular statements below the sketches, in which the body openings and the tail are listed in sequence. *Cephalodiscus* and *Ceratocystis* have identical sequences, except for the absence of the mesocoel pore in *Ceratocystis*. *Dendrocystoides* is the same as *Ceratocystis* except that the gonopore is out of sequence. *Trochocystites* agrees in sequence with *Ceratocystis*, although with no hydropore, gonopore or tail the sequence has only three members and the random probability of agreement is, in any case, an unimpressive 0.5. With *Kinzercystis*, without tail or gill slit, the random probability for four items is $1/13 = 0.17$. This in itself is no more than suggestive of dextrothetism, but for quinqueradiate echinoderms in general the evidence for dextrothetism does not depend on the topology of the adults, being firmly based on embryology. The major conclusion from text-figure 21 and from embryology is that all the five animals except *Cephalodiscus* have undergone the dextrothetic rotation in their ancestry.

(2) *Failure of the aulacophore theory.* The homology of the tail of *Dendrocystoides* with that of cornutes is confirmed by evidence of the brain and left trigeminal ganglion (see especially pl. 1, figs. 12, 13) at the proximal end of the tail in *Dendrocystoides*, as well as by the division of its tail into fore, mid and hind tail and the quadriserial arrangement of the fore-tail plates. If the tail of solutes is homologous with that of cornutes, then Ubaghs' interpretation of the tail as an aulacophore or feeding-arm cannot be correct. This conclusion is confirmed by difficulties in interpreting the mitrate tail as a feeding arm since one of the leading advocates of the aulacophore theory now accepts that the hind-tail plates of mitrates could not open at the mid line in life (Parsley 1988).

(3) *Homology of the hemichordate stalk and the chordate tail.* Evidence that the early solute *Castericystis* could attach when young to hard surfaces by the distal end of its tail strongly suggests that this tail was homologous with the stalk of *Cephalodiscus* (which has a sucker at the distal end). If the pterobranch stalk is homologous with the chordate tail, and if echinoderms are the extant sister group of chordates, then the echinoderms must have lost the tail in their early phylogeny.

(4) *Similarity of body plan in cornutes and solutes.* If the solutes are orientated as here suggested with the arm at anterior right, then their basic body plan is seen to resemble that of cornutes with the mouth at anterior right, the anus posterior in the head and right of the tail, the gill slit at posterior left in the head, and the flatter surface of the head ventral.

(5) *The phylogenetic position of the solutes.* Solute had a branchial slit (at least in *Dendrocystoides*), a water vascular system and a tail and in all these respects resembled hemichordates (in which the water vascular system is referred to as the left mesocoel). They were, however, dextrothetes, since they show signs of dextrothetism and had a calcite skeleton. They differed from the stem-group chordates called cornutes by retaining the water vascular system. And they differed from recognized stem-group echinoderms (except possibly the cinctans) in retaining the tail. The latest common ancestor of echinoderms and chordates would have had a tail, a branchial slit and an arm and therefore, if it were ever found, would be placed in the Soluta. The solutes, therefore, straddled the phylogenetic separation between echinoderms and chordates and so, to use Hennig's term, were an invalid stem group of the Dextrothetica. Further work will be needed to put the known solutes in their correct stem groups.

Acknowledgements. I am grateful to my colleague Andrew Smith for telling me, forcibly, that *Dendrocystoides scoticus* was the next animal to study. I am also grateful to a small group of devoted Scottish collectors – Mrs Eliza Gray and her daughters Alice, Agnes and Edith Gray, and Dr Archie Lamont and Mr James Begg – who, between 1880 and about 1940, accumulated the material on which this study is based (Cleavelly, Tripp and Howells, 1989). Dr Keith Ingham kindly gave me access to the collections of the Hunterian Museum, Glasgow, and David Lewis was a constant help at the British Museum (Natural History) and made up the plates. I thank my students Tony Cripps, Paul Daley, Fritz Friedrich, and Ian Woods for their moral support and their patient attempts to educate me.

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Typescript received 10 April 1989

Revised typescript received 20 August 1989

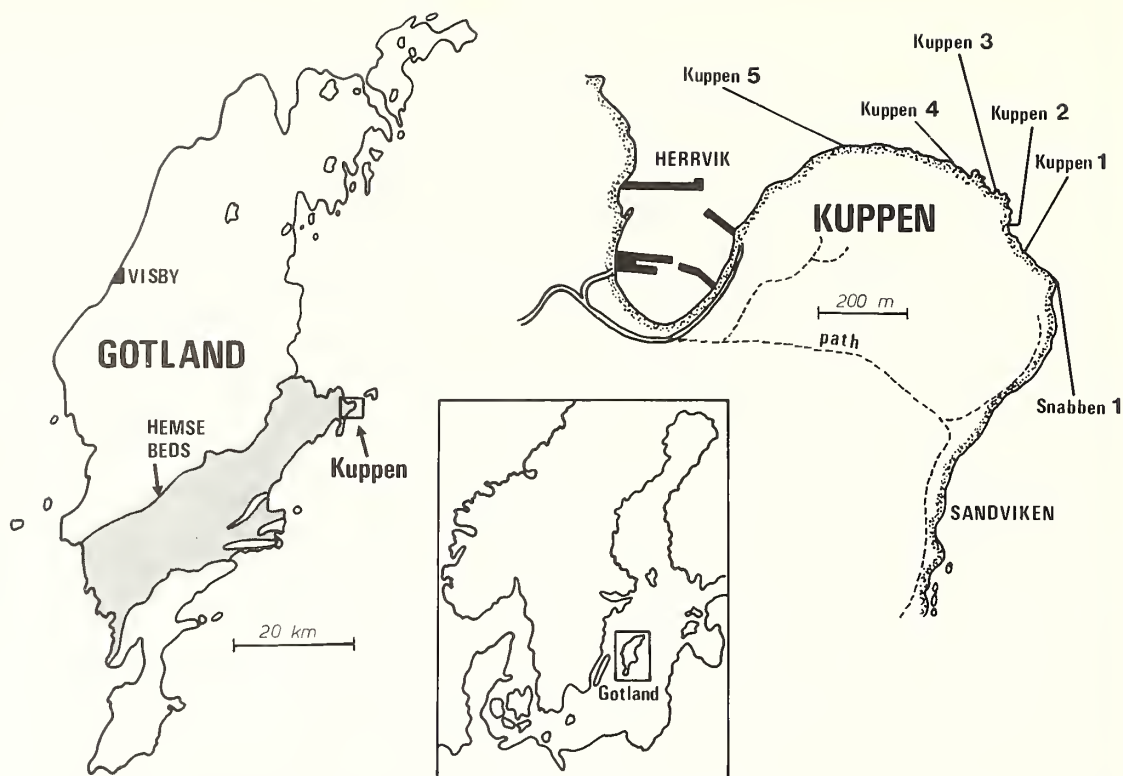
STROMATOPOROID PALAEOBIOLOGY AND TAPHONOMY IN A SILURIAN BIOSTROME ON GOTLAND, SWEDEN

by STEPHEN KERSHAW

ABSTRACT. A well-exposed stromatoporoid biostrome in the Hemse Group (middle Ludlow) of Gotland, Sweden, displays a wide range of stromatoporoid morphologies distributed amongst 16 species. The most abundant species, *Clathrodictyon mohicanum* Nestor has a laminar to low domical form, often of large size, distributed throughout the biostrome. Fast lateral growth is suggested to account for its abundance and commonly large size, its profile being suited to the normally low to moderate energy environment envisaged for the biostrome. Several other species adopted a similar growth style but were less successful; yet others, such as *Plectostroma intermedium* Yavorskyi, show a range of growth form from low to high domical shape, suggesting a phenotypic plasticity of growth form of each of these species. However, the range simply reflects the fact that individuals grew taller with age. Most laminar to low domical stromatoporoids at Kuppen are intact, but taller forms were frequently damaged and overturned by periodic storm action, indicating that a lower profile was clearly an advantage. Some species show variations in distribution of undamaged forms horizontally between, and vertically within, localities; there is evidence that some responded to environmental gradients, notably turbulence and sedimentation. Most grew on a stable substrate provided by dead skeletons of other stromatoporoids. Under cathodoluminescence stromatoporoid skeletons show speckled dull and bright luminescence, an identical signal to the pelmatozoan debris found in the biostrome, circumstantial evidence for an original mineralogy of high Mg calcite in both.

RECENT advances in studies of stromatoporoid palaeoecology have focused attention on the importance of recognizing the degree to which genetics controlled growth form (Cornet 1975; Kershaw 1981; Stearn 1984) and this study examines these features in an excellent example of a stromatoporoid biostrome at Kuppen on southeast Gotland, Sweden (text-fig. 1). The biostrome was the subject of an earlier paper (Kershaw 1981) which demonstrated that low profile and high profile forms were created by different stromatoporoid species. However, that study was biased in its collecting, by selecting particular morphologies and at only one site on a biostrome which is exposed continuously for nearly one km laterally. Thus it was not possible to determine whether species were truly limited to particular growth forms or instead were capable of producing a range of morphologies.

In this study, a total sample of approximately 400 stromatoporoids collected from several points along the length of the biostrome provides comprehensive information on the distribution of stromatoporoids and the relationship between species and their morphotypes. Morphotypic variation is shown to be greater than that discovered in the earlier study, but is related to growth histories of individual stromatoporoids, and the interpretation of a genetic control on growth form is confirmed. Also, as the biostrome accumulated, storms selectively damaged some growth forms and certain species, and allow useful observations on the palaeoenvironment and palaeobiology of the stromatoporoids to be made. Lithification history of the biostrome and cementation of stromatoporoid skeletons are briefly examined to enhance the taphonomic interpretations. The information obtained from the study provides an insight into growth styles of different stromatoporoid species, controls on their forms, and indicates the use of stromatoporoids in determining features of the palaeoenvironment, particularly with regard to sedimentation and turbulence.



TEXT-FIG. 1. Location of the Kuppen biostrome within the Hemse Beds (stippled) on Gotland. Sampling localities are shown, details of which are filed at the Allekvia Field Station on Gotland and based on the locality system devised by Laufeld (1974a). Material used for this study is deposited with the Swedish Geological Survey, Uppsala.

GEOLOGICAL SETTING

The Silurian sediments of Gotland have been viewed as deposited in a carbonate platform setting (Kaljo 1970, Laufeld and Bassett 1981), but with evidence of a carbonate ramp (Frykman 1989) in the Baltic area, and record several transgressive and regressive sequences in which argillaceous limestone formations alternate with biohermal and biostromal limestones (Riding 1981).

The Hemse Beds (middle Ludlow) of Hede (1960) comprise calcareous mudstones towards the west, the Hemse Marl, and stromatoporoid-dominated biostromal and biohermal limestones in the east. The precise stratigraphic relationship between the muds and limestones is unclear. A generally southwest dipping palaeoslope has been envisaged by Martinsson (1967, p. 383) for much of the Gotland sequence, and the Hemse Marl facies are estimated to have been deposited in deeper water than the limestones (Laufeld 1974b). However, work with orthoconic nautiloids has shown conflicting probable shoreline trends in the Hemse Beds. Laufeld (1974b) interpreted current flow in their southwestern outcrops to be perpendicular to the Ludlovian shoreline which he interpreted to have an ENE–WSW trend, with open sea generally to the south. However, Sundquist (1982a) presented rose diagrams of bipolar nautiloid orientations for the Grogarnshuvud localities, 3 km NW of Kuppen, which show orientations at approximately 90° to Laufeld's. This suggests an approximate NW–SE shoreline in this area. These results are not necessarily incompatible because there may have been local variations in shoreline trends or current flow directions.

Shallow water facies are common in the eastern outcrops of the Hemse Beds. Ripple marks at

Gannes, 5 km west of Kuppen (Sundquist 1982*b*) are interpreted to have formed in water of about 10 m depth; Manten (1971, pp. 353, 379) reported erosion surfaces at Gannes. Cherns (1982) identified palaeokarsts, erosion surfaces and stromatolites in the overlying Eke Formation, and Cherns (1983) indicated shallow water facies at the Hemse-Eke boundary.

Biostromes 0.5–c. 10 m thick are widespread in the southeast Hemse Beds, interbedded with shales, skeletal grainstones and rudstones. Such thinly bedded deposits, with shallow water associations, exhibit common vertical facies changes illustrative of a sea level fluctuating relative to sea bed. Lateral facies changes occur also, clearly demonstrable at Kuppen; there a facies mosaic is developed, termed here the Kuppen facies complex. A brief description of the complex follows, providing a background to interpretation of the stromatoporoid distributions and growth forms.

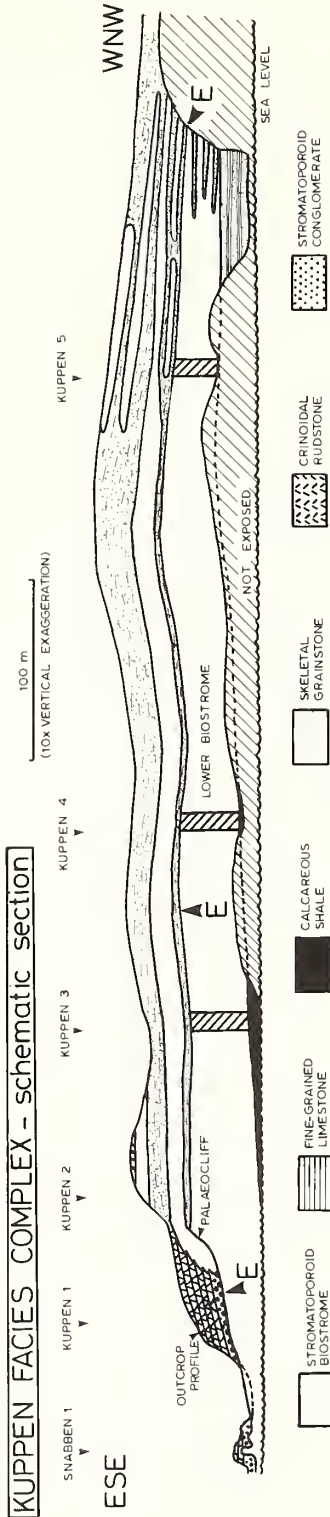
THE KUPPEN FACIES COMPLEX

The complex consists of several biostromes interbedded with argillaceous limestones, stromatoporoid conglomerates and crinoidal grainstones (text-fig. 2); the lowest biostromes is studied here. Stromatoporoid biostromes crop out in neighbouring areas, but only those at Kuppen were examined. Riding (1981, p. 65) recognized the biostromes as distinct from other organic build-ups on Gotland and applied the term 'Kuppen reef type'. He provided a log of the vertical facies changes at locality Kuppen 2 (see text-fig. 2), and noted lateral variations in the complex. Text-fig. 3 illustrates important selected features of the facies and displays the general character of the stromatoporoid morphologies.

As shown in text-fig. 2, the sequence begins with a poorly exposed argillaceous limestone containing a sparse stromatoporoid fauna. The overlying biostromes (from which the sample was collected) has, in most places, a crinoidal limestone basal bed, 30–50 cm thick, with stromatoporoid debris and some large stromatoporoids *in situ*. Pressure solution has extensively affected the stromatoporoids in places, such that in many the original morphology is unrecognizable. Biostromes sediment is most micritic fill between stromatoporoids, with lesser amounts of bioclastic material. The biostromes varies in thickness from 2.5–4 m and is everywhere terminated by an erosion surface, much of which is prominent and planar (text-fig. 3A and C; Munthe 1910, fig. 28); stromatoporoids are truncated, indicating that they were cemented into the matrix prior to erosion. An indeterminate amount of the upper section of the biostromes has been removed, and the erosion surface becomes more irregular towards the ESE, (text-fig. 3A). Minor sea level fluctuations could account for the vertical facies changes. The sequence is similar to the model provided by James (1984, p. 220) of shallowing-upwards carbonate units and to the example studied by Wilson (1967) in Devonian limestones of the Williston Basin of N. Dakota. Gypsum crystals in the upper part of the biostromes suggest the possibility of hypersaline conditions during a stage in the development of the biostromes (Kershaw 1987*a*), but no corroborative sedimentological evidence exists due to erosion of the top of the biostromes.

Dipping beds at Kuppen 1 are attributed to deposition on a slope associated with the palaeocliff (text-fig. 2), while undulation of bedding in the remainder of the complex is probably due to settling of the sediments on the shale at the base of the complex. There is only a slight tectonic dip across Gotland and the complex evidently formed on an approximately flat-lying sea bed. Lack of siliciclastics suggests a low hinterland, and consequently little terrigenous sediment transport into the area during the development of the complex. The SE area contains coarse skeletal limestones, whereas the NW areas with thin, interbedded, finer-grained limestone facies were quieter.

The current energy affecting the complex clearly varied. Most tall domical stromatoporoids are now on their sides, indicating that energy was relatively low to moderate while they were alive, but periodically sufficient to topple them. Substantial amounts of stromatoporoid debris also indicate higher energy events. The biostromes has the appearance of a mixed fauna (text-fig. 3), with many large stromatoporoids not disturbed from growth position, while debris was piled around them. Further thin biostromes interleaved with bedded limestones overlie the lower biostromes (text-fig. 2), but were not studied in detail. However, there are some differences in fauna; for example, the



TEXT-FIG. 2. Schematic section through the Kuppen facies complex showing vertical and lateral facies distribution dominated by stromatoporoid biostromes. Note the undulating erosion surface (E) truncating the top of the lower biostrome, with irregularities at the southern end of the outcrop, where small penecontemporaneously eroded stacks are present at Snabben 1. Here the biostrome is overlain by stromatoporoid conglomerate and crinoidal grainstones. Elsewhere, it is succeeded by interbedded biostromes and skeletal limestones. The lower biostrome thins to the WNW and is interrupted by skeletal grainstone beds. Hatched areas are sampling sites for stromatoporoids. Vertical exaggeration 10 ×.

biostrome overlying that studied here has a greater abundance of tabulate corals, particularly favositids.

Diagenesis

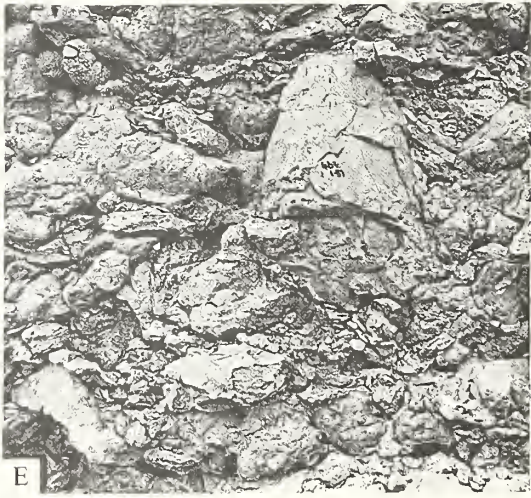
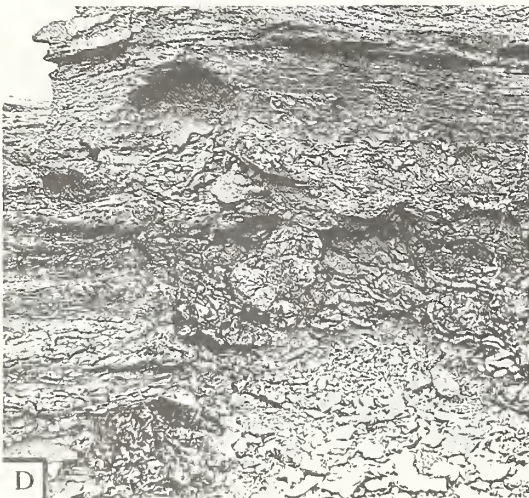
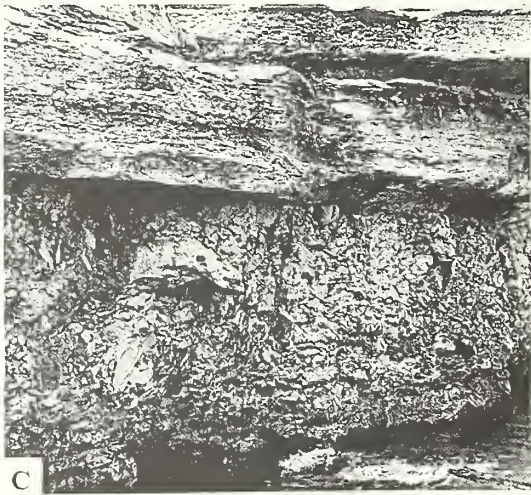
A full description of diagenesis of the biostrome is inappropriate here, but some aspects pertain to a taphonomic assessment of the stromatoporoids, so an outline of the important events is given. Three cement stages are recognized in both bioclastic fill and stromatoporoid galleries (text-fig. 4).

First stage cement forms non-luminescent (under cathodoluminescence – CL), non-ferroan syntaxial calcite on pelmatozoan debris. It is also present sporadically in stromatoporoid skeletal galleries (text-fig. 4B, D) and is most likely to be meteoric cement formed during uplift. Syntaxial cement on pelmatozoans is commonly regarded as meteoric because high Mg levels in sea water prevent its growth there; meteoric water is low in Mg. In the present sample, such cement fills most of the pore space of pelmatozoan grainstones, and leaves little doubt that it is of meteoric origin. There was apparently little marine cement, and this is corroborated by the common occurrence of toppled tall stromatoporoids. As noted by Kershaw (1981) some were toppled during life and show reorientated growth directions.

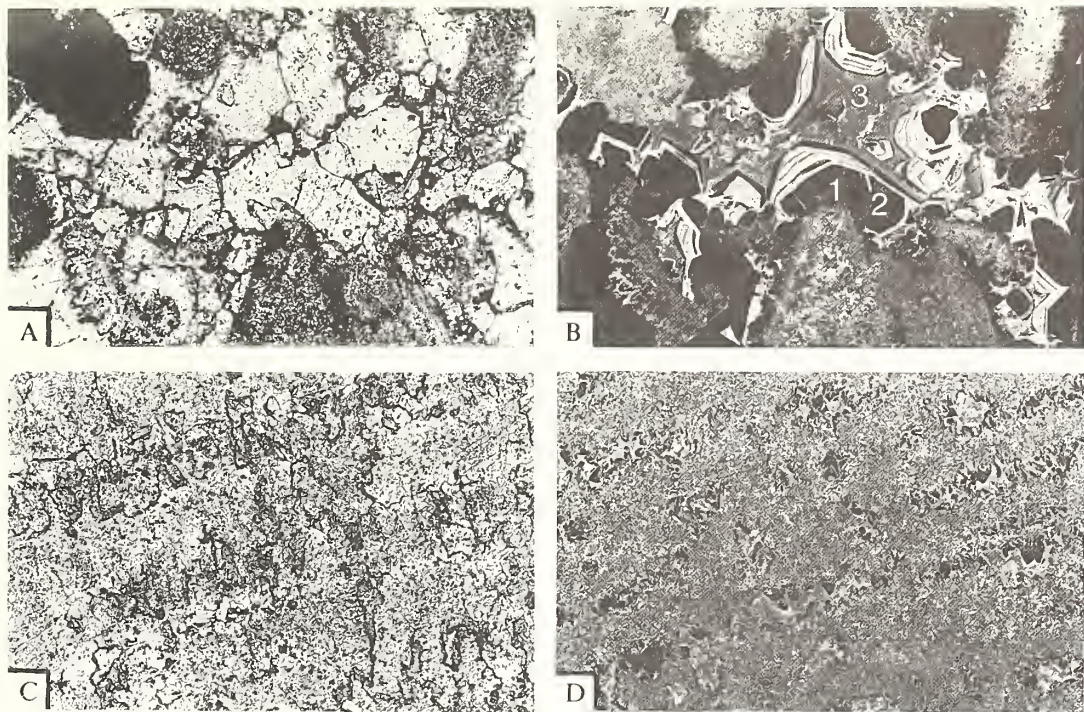
Second stage cement comprises very thin alternating bright and non-luminescent bands suggestive of subsequent burial near the redox boundary, with cyclic recharge of oxygenated water, a common situation in limestones (Scoffin 1987, p. 129). Staining of the same thin sections that were used for CL examination shows that these areas of the sections are also non-ferroan, which is consistent with the interpretation of such banded cement (under CL) being generated by the presence (bright) and absence (dark) of manganese, but with no iron present. The absence of iron is usually regarded as being due to its combination with sulphides liberated by action of sulphate-reducing processes on porewater sulphates in shallow burial, so that it is unavailable for inclusion into calcite lattices (Scoffin 1987, p. 129). This cement is again best developed in the porous pelmatozoan grainstone deposits and to a lesser extent in stromatoporoid skeletal galleries.

The final cement is dull luminescent and ferroan, where iron, now incorporated into the calcite cement following depletion of sulphides in pore waters, partially counteracts the bright CL effect of manganese (referred to as quenching). This cement, which probably indicates deeper burial, occupies the small remaining pore space in grainstones. However, most of the pore space of stromatoporoid galleries is usually filled with dull luminescent, ferroan cement, suggesting that it grew slowly at depth, after the biostrome had been buried. Since they represent largely closed porosity, stromatoporoid galleries are likely to have been less accessible to earlier pore waters. Comparable luminescent zones were observed by Dorobek (1987) in late Silurian – early Devonian carbonates in the Appalachians.

Stromatoporoid skeletons show a similar CL response to the pelmatozoan debris in the biostrome (text-fig. 4B, D). Also, all stromatoporoids in the assemblage are partially recrystallized. General observations by myself and other authors (Stearn, pers. comm. 1988; Watts 1981; Wood 1987) indicate that many stromatoporoids did not recrystallize as completely as aragonitic shells of molluscs, yet are consistently more recrystallized than the low Mg calcite of brachiopods. The inference that these stromatoporoids were therefore high Mg calcite originally is supported by a) the similarity of response in CL to pelmatozoans (high Mg calcite) and b) the widespread occurrence of microdolomite rhombs in stromatoporoid skeletons at Kuppen. Lohmann and Meyers (1977) discussed a burial diagenetic process whereby Mg expelled from high Mg calcite skeletons form localized dolomite. CL response and dolomite occurrence may of course be due to other diagenetic processes, but the partial recrystallization widespread amongst Silurian and Devonian stromatoporoids argues against low Mg calcite or aragonite original compositions. There is a wider issue of variation of stromatoporoid skeletal mineralogy through geological time and in relation to taxonomy, which requires investigation.



TEXT-FIG. 3. For legend see opposite.



TEXT-FIG. 4. Thin section views of typical material from the lower biostrome. A. Plane polarized light view of crinoidal grainstone from Kuppen 3A. B. Cathodoluminescence response of the same area, showing three zones of cement growth: 1. non-luminescent syntaxial cement on crinoids; 2. alternating bright and non-luminescent cements; 3. dull cement. Note the bright, dull and dark-speckled appearance of the crinoid fragments. C. Plane polarized light view of recrystallized stromatoporoid skeletal material of *Stromatopora venukovi* with crystal boundaries of neomorphic cement cutting across the stromatoporoid structure. The preserved laminae and pillar structure are difficult to recognize at this magnification, but galleries are discernible as sparry patches. D. Cathodoluminescence response of the same area shows the three cement zones in the galleries, plus a speckled luminescent character of bright, dull, and dark areas in the stromatoporoid skeleton. See text for discussion. All photos $\times 35$.

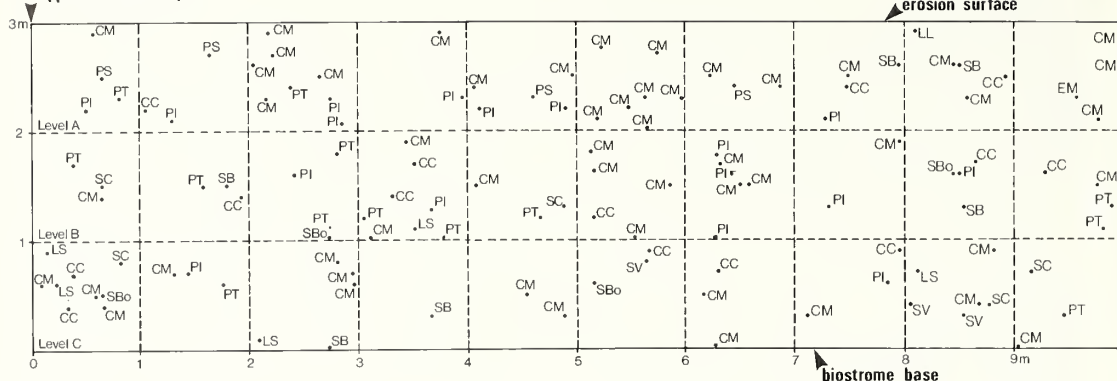
FOSSIL ASSEMBLAGE OF THE LOWER BIOSTROME

Three accessible localities selected for intensive sampling are Kuppen 3, 4 and 5 (text-figs. 1 and 2), where the biostrome is 3.4, 3 and 2.5 m thick, respectively.

At each locality a grid was drawn on the vertical cliff face, 10 m long and of variable height depending on the thickness of the biostrome at that place. Each was divided into three parts parallel

TEXT-FIG. 3. Photographs of selected parts of the Kuppen biostrome. A. Cliff face at Kuppen 5 showing basal bioclastic bed and densely packed stromatoporoids in the biostrome; length of view 8 m. B. Interbedded shales and limestones overlain by thin biostromes and limestone bands at the northwestern end of Kuppen; length of view 3.5 m. C. Biostrome at Kuppen 1, undercut by the sea where shale underlies the biostrome, and sharp erosion surface overlain by crinoidal gravel. Note the large, low domical stromatoporoid centre left in biostrome; length of view 5 m. D. Eroded stack (top left in hollow) at the biostrome top at Snabben 1, surrounded by stromatoporoid conglomerate and crinoidal gravel; length of view 3 m. E. Vertical section of central part of biostrome at Kuppen 4 (see text-fig. 5), showing laminar, low to high domical, broken and stylolitized stromatoporoids; length of view 0.95 m.

Kuppen 4 reference point



TEXT-FIG. 5. Schematic vertical section of the lower biostrome at Kuppen 4 to demonstrate sampling method. A. Sample locations of identified species, determined by vertical and lateral coordinates derived from random number tables. B. Morphology of the stromatoporoids sampled, illustrated in their preserved attitudes and positions. Three categories of preservation of growth form are recognized: *c* = complete specimens; *b* = broken skeletons, including small fragments; *s* = specimens so badly affected by pressure solution (stylolites) to make impossible any distinction between originally complete or broken. Specimens not identified are omitted from the diagram. Text-fig. 3E (inset) shows the general character of the outcrop. Stromatoporoid species are abbreviated in this and other diagrams, as follows. LL = *Labechia lepida*, CC = *Clathrodictyon convictum*, CM = *C. molicanum*, EM = *Ecclinadictyon macrotuberculatum*, PK = *Plexodictyon katriense*, DY = *Diplostroma yavorskyi*, PS = *Plectostroma scaniense*, PI = *P. intermedium*, SB = *Stromatopora bekkieri*, SC = *S. carteri*, SL = *S. lamellosa*, SV = *S. venukovi*, SBo = *Syringostromella borealis*, PT = *Parallelostroma typicum*, LS = *Lophiostroma schmidtii*.

to bedding, here termed levels, of approximately equal thickness and labelled A, B, C, respectively from top to bottom (text-fig. 5). Bedding planes do not exist within the biostrome and so the level boundaries are artificial. Therefore levels are not necessarily time equivalent between localities.

Within each level, stromatoporoids were collected using random number tables to determine the precise collecting point and to obtain a representative sample of the assemblage (text-fig. 5). The

intention to collect 50 samples from each level at every locality was not possible and the final sample consisted of 404 specimens. Kuppen 5A was the worst affected with only 18 pieces retrieved. Of the total, 60 were unidentifiable, but these were evenly spread across sample sites (average of five in each) except in the case of Kuppen 3B, where 13 of 48 collected could not be classified. Thus the overall distribution of identified stromatoporoids is not unduly affected by the presence of unidentified samples. Almost all samples collected are stromatoporoids, with few corals. Heliolitids, however, are common in places, whereas favositids are rare. Kershaw (1987b) showed that 10% of stromatoporoids in this biostrome contain symbiotic corals; further samples revealed that in fact 20% of the stromatoporoid assemblage contains a variety of rugose corals and syringoporids, although this is unevenly distributed within the biostrome. Various other taxa, particularly echinoderms, are present as debris.

Since collecting was random, the data set provides a representative sample of the assemblage, and allows comparison within and between localities to furnish information on vertical and horizontal variation.

Stromatoporoid assemblage

Sixteen species distributed amongst several orders of stromatoporoids were found. Taxonomic revision by Stearn (1980) produces differences from the scheme applied by Mori (1969, 1970) to Gotland stromatoporoids which was used also by Kershaw (1981). Stearn's division into several orders is adopted here, giving the following list for the biostrome:

Order Lophiostromatida: *Lophiostroma schmidtii* (Nicholson)

Order Labechiida: *Labechia lepida* Mori

Order Actinostromatida: *Plectostroma scaniense* Mori, *P. intermedium* Nestor, *Pseudolabechia granulata* Yabe and Sugiyama

Order Clathrodictyida: *Clathrodictyon mohicanum* Nestor, *C. convictum* Yavorsky, *Ecclimadictyon macrotnberculatum* (Riabinin), *Plexodictyon katriense* Nestor, *Diplostroma yavorskyi* Nestor

Order Stromatoporida: *Stromatopora bekkeri* Nestor, *S. carteri* Nicholson, *S. lanuella* Yavorsky, *S. venkovii* Yavorsky, *Syringostromella borealis* (Nicholson), *Parallelostroma typicum* (Rosen).

These species are all well-known Palaeozoic forms and since they are fully described by Nestor (1966), Mori (1969, 1970), Stock (1979) and Stock and Holmes (1986), there is no need to illustrate them here. However, worth noting is that stromatoporoid classification is based on microscopic characters of laminae and pillar structure and arrangement. Two thin sections (vertical and horizontal) are required per specimen. The shape of the entire skeleton is not a diagnostic character, although some species are limited to certain shapes. Most species in the present sample are distinctive, but some raise taxonomic problems that are briefly discussed below.

Most specimens of *Stromatopora bekkeri* and *Parallelostroma typicum* are distinct, but some show such variability of structure of skeletal elements that occasional difficulty was faced in deciding into which species they should be grouped. Fagerstrom and Saxena (1973) recognized that variations of stromatoporoid structure within single thin sections can be high, but all within a single distinct species. Stock (1979), Stock and Holmes (1986) distinguished several species of *Parallelostroma* in the Upper Silurian of eastern America, with minor, but consistent, differences in skeletal structure defining the species. This is not possible in the present specimens, where variation, often in different parts of the same thin section, produces laminae and pillar arrangements resembling both species. The taxonomic uncertainty generated by these observations means that the distinction between these two species is unreliable. The possibility that they represent phenotypic variants of a single species cannot be discounted, although they could represent two species with overlapping skeletal morphology, clearly causing havoc with the morphospecies concept as applied to these species. The validity of other species at Kuppen is not questioned since they show consistent differences of skeletal structure. For the present purposes, *P. typicum* and *S. bekkeri* have been distinguished as separate species in text-figs. 5, 6, 8, 9 and 10, and the uncertain examples omitted, pending a separate analysis of this problem.

TABLE 1. Distribution of numbers of specimens of all identified stromatoporoids from Kuppen, arranged according to locality and level, with the three categories of *c* (complete), *b* (broken) and *s* (badly affected by pressure solution) indicated.

Species	Kuppen 3									Kuppen 4									Kuppen 5									Total			
	Level A			Level B			Level C			Level A			Level B			Level C			Level A			Level B			Level C						
	c	b	s	c	b	s	c	b	s	c	b	s	c	b	s	c	b	s	c	b	s	c	b	s	c	b	s	c	b	s	
<i>L. schmidti</i>	—	—	—	—	—	—	4	—	1	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	5	—	—	15	—	1	
<i>P. typicum</i>	—	—	—	1	1	—	—	—	—	2	—	—	—	7	2	—	—	—	—	—	2	—	—	—	2	—	—	11	1	12	
<i>S. borealis</i>	6	1	—	1	—	1	1	—	—	—	—	—	1	—	1	2	—	—	—	—	—	—	—	—	—	—	—	11	1	2	
<i>S. venukovi</i>	—	—	—	—	—	—	3	—	1	—	—	—	—	—	—	2	—	1	—	—	—	—	—	1	2	—	—	6	2	2	
<i>S. lamellosa</i>	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	
<i>S. carteri</i>	1	—	—	1	1	—	1	—	—	—	—	—	1	1	—	1	1	—	—	—	—	—	—	—	—	—	—	4	3	2	
<i>S. beckeri</i>	1	1	—	4	3	—	8	3	1	1	1	—	—	2	1	—	1	—	—	4	1	2	3	—	1	22	9	7	—	—	
<i>P. granulata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>P. intermedium</i>	2	13	4	—	1	—	1	1	—	1	1	6	—	1	6	1	1	—	5	—	4	8	—	5	2	—	6	20	18	31	—
<i>P. scanense</i>	—	2	—	—	—	—	1	—	—	1	—	3	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	4	2	4	—
<i>D. yavorskyi</i>	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
<i>P. kariense</i>	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	—	1	—
<i>E. macrothuber- culatum</i>	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
<i>C. mollicanum</i>	6	—	—	14	1	—	13	1	1	21	—	3	9	3	1	11	3	1	—	—	7	—	1	8	1	2	89	9	9	—	—
<i>C. convictum</i>	—	—	—	—	—	—	—	—	—	3	—	2	—	4	3	2	—	2	—	1	3	—	3	5	—	3	18	2	11	—	—
<i>L. lepida</i>	2	—	—	4	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	1	2	—	—

Plectostroma scaniense is distinguished from *P. intermedium* only by possessing astrorhizae (Nestor 1966, pl. XI; Mori 1970, pl. X). Many authors have discussed the taxonomic significance of these structures, and there is disagreement about their importance (see Stearn 1980, Wood 1987 for reviews). Both species exhibit the same growth form characteristics. I would accept that they could be the same species, but have left them separate in case future work should show them to be distinct.

Stromatoporoid growth form

Table 1 shows the total identified sample, in each locality. Text-fig. 6 and Table 2 summarize the data into localities and levels for visual comparison. Division into three categories of preservation of the growth form (c, b, s; see Table 1) is important for morphological analysis. The most useful for morphological study are complete specimens (category c). Fragmented specimens (category b) are useful for studying biostratinomy, and specimens affected so badly by pressure solution that their shape cannot be determined (category s), were included to provide full information on specific distribution. Pressure solution effects are more pronounced at Kuppen 5 than at the more southerly localities. Dimensions of broken and stylolitized specimens were not recorded in the field; both are generally small, of the order of 10 cm in size, although larger specimens occur.

Growth forms fall into a relatively simple range from laminar to extended domical and bulbous of Kershaw and Riding (1978, 1980), illustrated in text-fig. 7. Most stromatoporoids have smooth outlines and rarely show ragged edges (where sediment periodically covered the flanks of skeletons). Within smooth outlines, laminae show different growth patterns. Some are completely *enveloping*, in which successive laminae cover all earlier laminae; others are *non-enveloping*, where growth produced additions at the apex and extended only a short distance down the flanks. Others have a combination of the two, and in these, lower stages of growth were enveloping while later growth was

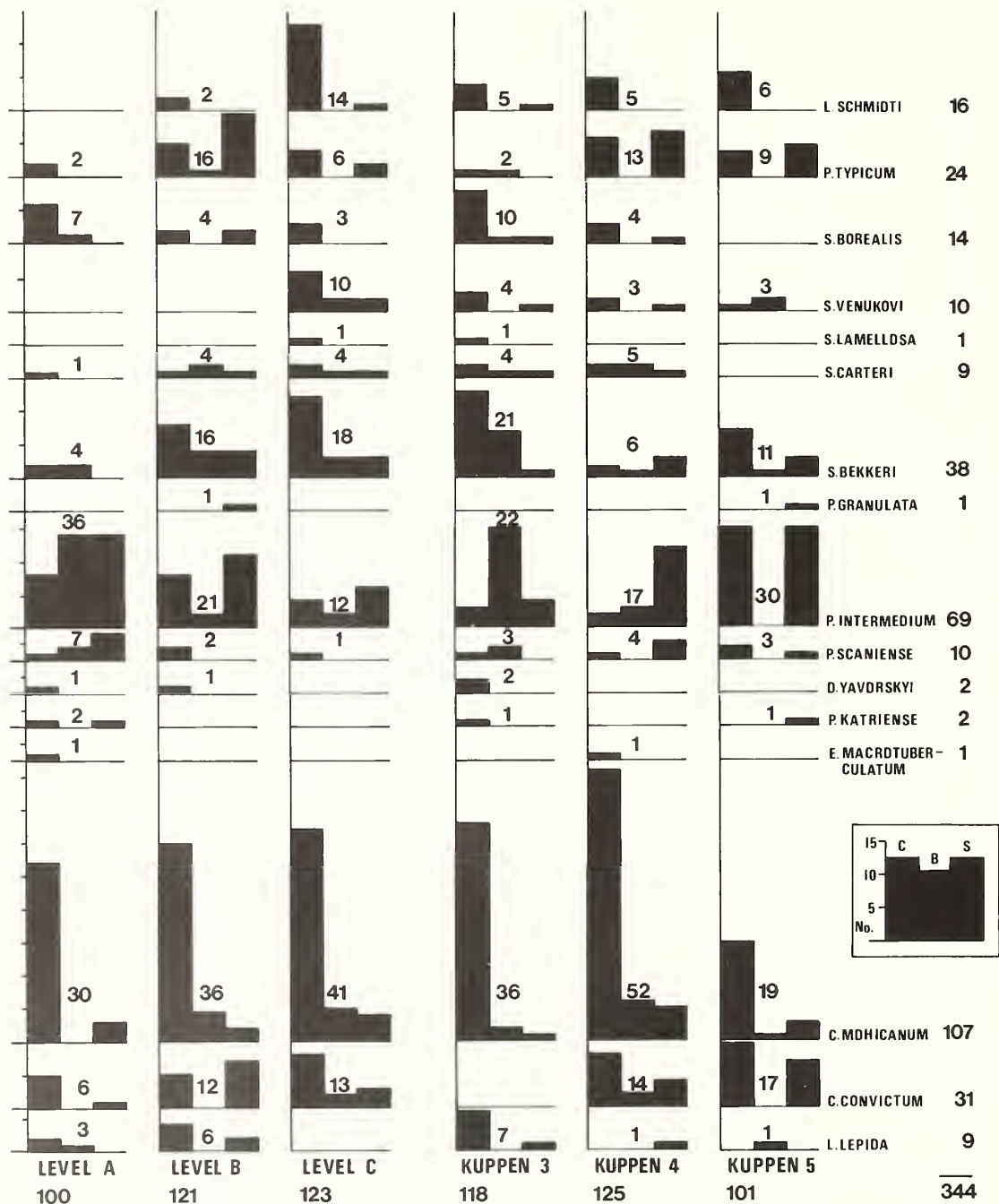
TABLE 2. Distribution of numbers and percentages of complete specimens at Kuppen; note the large decrease of *Clathrodictyon mohicanum*, and increase of *Plectostroma intermedium* from Kuppen 4 to 5.

Species	Numbers of complete specimens							
	Kuppen 3		Kuppen 4		Kuppen 5		Total	
	No.	%	No.	%	No.	%	No.	%
<i>L. schmidtii</i>	4	5.1	5	6.8	6	10	15	7.1
<i>P. typicum</i>	1	1.3	6	8.2	4	6.7	11	5.2
<i>S. borealis</i>	8	10.3	3	4.1	—	—	11	5.2
<i>S. venukovi</i>	3	3.8	2	2.7	1	1.7	6	2.8
<i>S. lamellosa</i>	1	1.3	—	—	—	—	1	0.5
<i>S. carteri</i>	2	2.6	2	2.7	—	—	4	1.9
<i>S. bekkèri</i>	13	16.7	2	2.7	7	11.6	22	10.4
<i>P. granulata</i>	—	—	—	—	—	—	—	—
<i>P. intermedium</i>	3	3.8	2	2.7	15	25	20	9.5
<i>P. scaniense</i>	1	1.3	1	1.4	2	3.3	4	1.9
<i>D. yavorskyi</i>	2	2.6	—	—	—	—	2	0.9
<i>P. katriense</i>	1	1.3	—	—	—	—	1	0.5
<i>E. macrotuberculatum</i>	—	—	1	1.4	—	—	1	0.5
<i>C. mohicanum</i>	33	42.2	41	56.3	15	25	89	42.3
<i>C. convictum</i>	—	—	8	11	10	16.7	18	8.5
<i>L. lepida</i>	6	7.7	—	—	—	—	6	2.8
	78		73		60		211	

KUPPEN STROMATOPOROID DISTRIBUTION

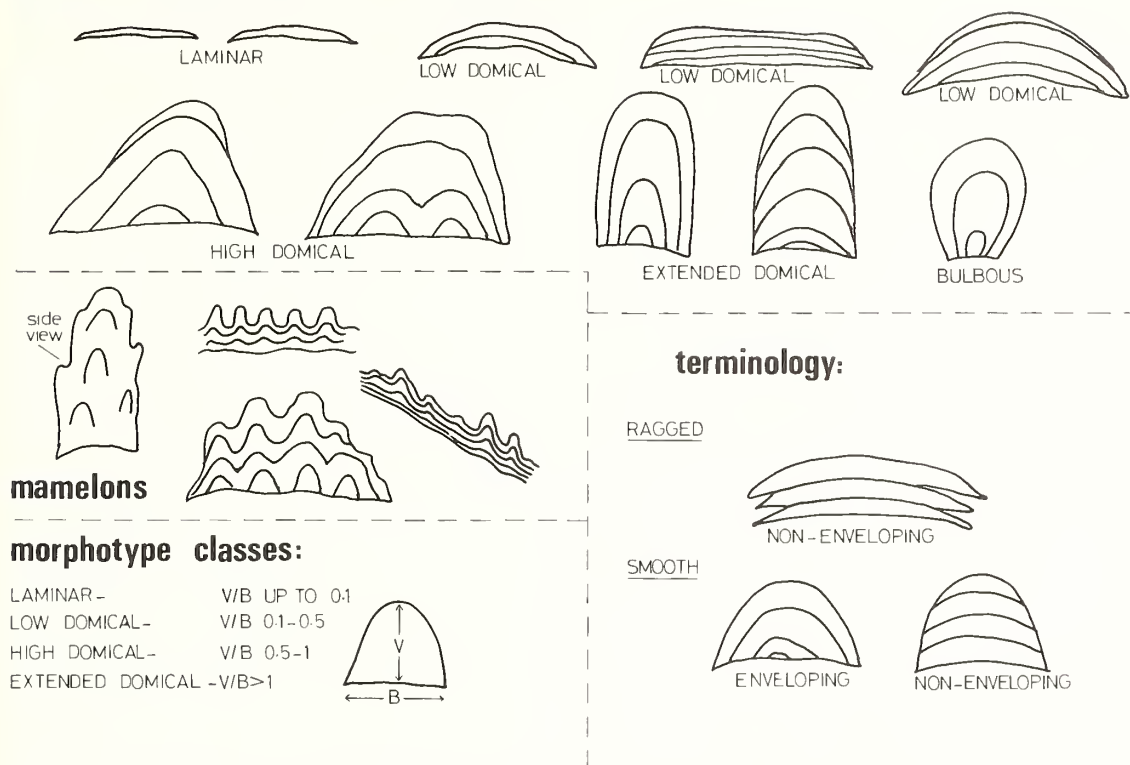
A. levels

B. localities



TEXT-FIG. 6. For legend see opposite.

Kuppen stromatoporoid morphotypes



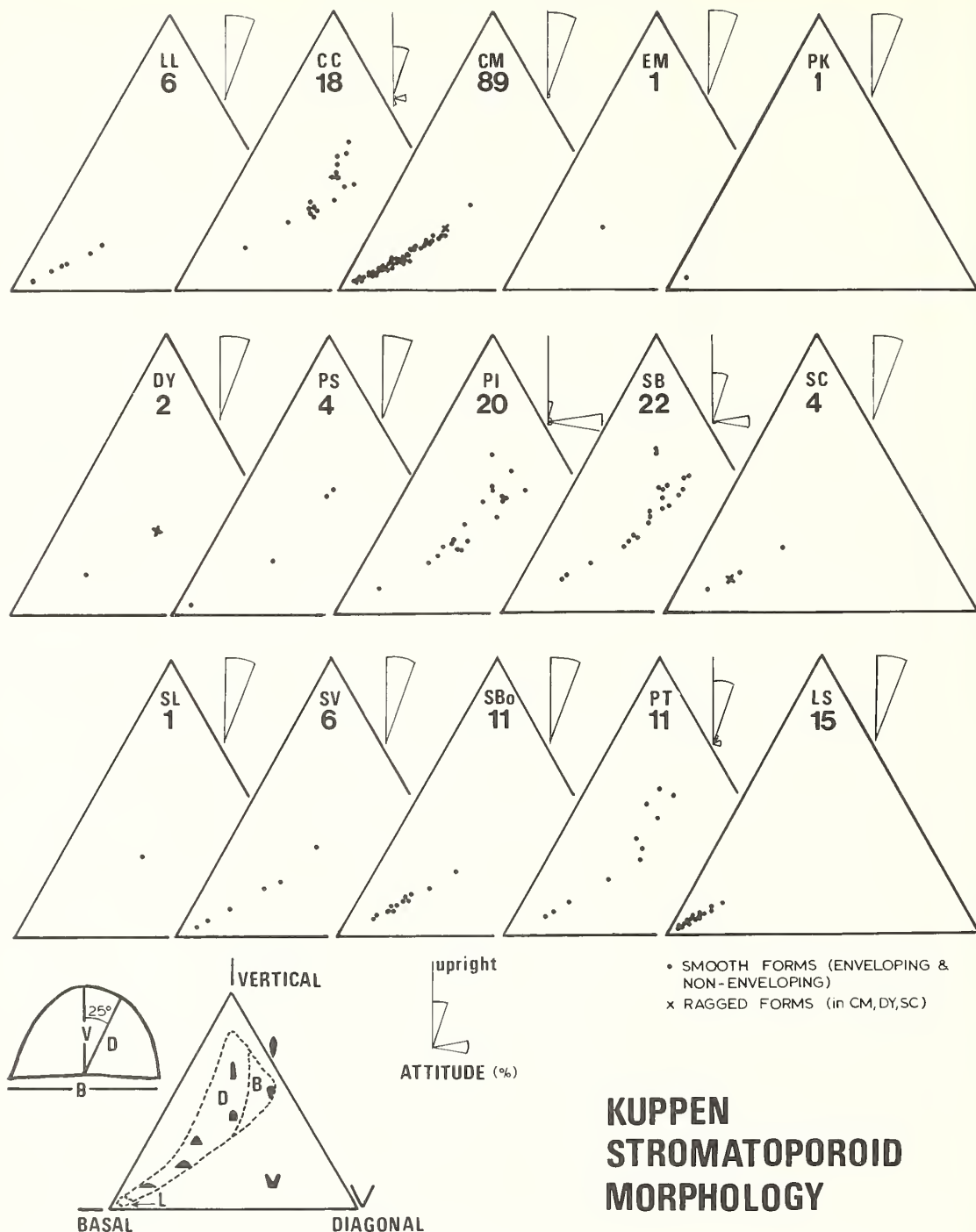
TEXT-FIG. 7. Stromatoporoid morphotypes in the lower biostrome, showing a range from laminar to extended domical and bulbous, together with morphotype classification and terminology applied to the forms. These shapes are typical, simple, Silurian forms, shown in vertical section except where indicated. All growth forms can possess either enveloping or non-enveloping laminae. Very few are ragged and some show well developed mamelons.

non-enveloping. All three variations of smooth outlines are found in each of the more abundant species.

Attempts to quantify these features proved unrewarding; to determine the extent of enveloping and non-enveloping laminae in individual stromatoporoids requires medial vertical sections through skeletons. Only some specimens are suitably broken open in outcrop, and many individuals are displayed entire, obscuring the internal patterns. Therefore it has not been possible to determine the degree to which each style is developed at Kuppen, and graphical representations of morphology in the present study necessarily ignore these patterns in smooth stromatoporoids.

Because of the range of simple morphologies at Kuppen, the use of the parameterization scheme devised by Kershaw and Riding for graphically displaying stromatoporoid morphotypes is

TEXT-FIG. 6. Graphical representation of the distribution of specimens of identified stromatoporoid species in the lower biostrome. The same data are arranged in two ways to illustrate vertical and horizontal variations. A. All specimens in each level. B. All specimens in each locality. Specimens are grouped into categories *c*, *b* and *s* according to the preservation of their growth form; see caption of text-fig. 5. Note abundance of *Clathrodictyon mohicanum*, and lesser amounts of *Plectostroma intermedium*, *Stromatopora bekkeri*, *Parallelostroma typicum*, *Clathrodictyon convictum*, *Syringostromella borealis* and *Lophiostroma schmidti*.



TEXT-FIG. 8. Triangular displays of morphology of all complete stromatoporoids in the lower biostrome, plotted using the Kershaw and Riding (1978) scheme. Morphology varies little between localities and levels in the biostrome, so species are illustrated grouped together. Inset shows measurements of basal diameter (B), vertical height (V) and diagonal length (D), and the morphological fields generated by the display. Partial rose diagrams of attitudes of skeletons are provided.

appropriate. Text-fig. 8 shows the plotted forms of all complete specimens; fragmented and stylolitized examples cannot be represented.

Text-fig. 8 shows that while many species, such as the ubiquitous *C. mohicanum*, are restricted to the lower profile fields, other species show a range of form from low to extended domical and bulbous. This suggests a phenotypic plasticity of the growth form of these species. *S. bekkeri* also seems not to be restricted to tall growth form as suggested by Kershaw (1981).

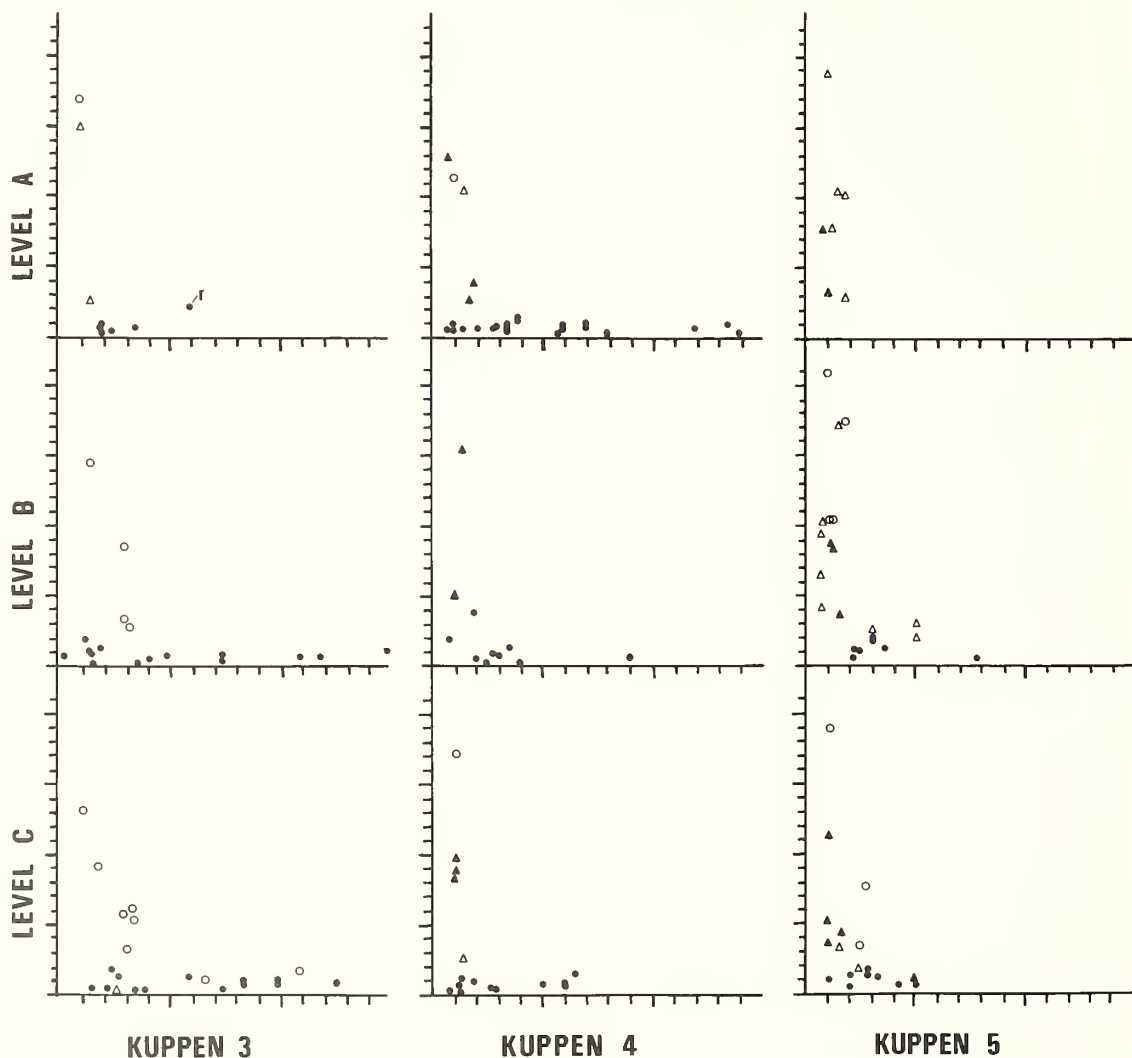
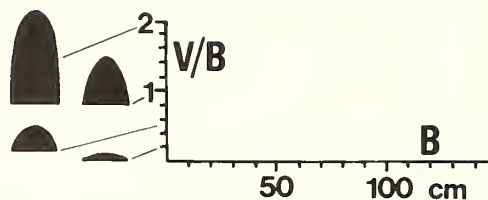
However, these displays take no account of the overall dimensions of skeletons. Since most growth forms plot on a line emanating from the basal corner, the most important components of the stromatoporoid morphology at Kuppen are B and V, with D having less effect. Therefore the V/B ratio in these specimens provides a crude measure of shape, and when plotted against B (text-figs. 9, 10), two clear trends are revealed in the more abundant species. For low profile forms, low B values are usually accompanied by low V/B ratios; but at higher B values, V/B stays low. For those species which can have taller forms, the graphs show that low B values are also accompanied by low V/B ratios, but at higher V/B ratios, B is still low (text-fig. 9). Furthermore, examination of early growth stages in the stromatoporoids shows those of tall forms to be low profile. Thus *Plectostroma intermedium*, *Clathrodictyon convictum*, *Parallelostroma typicum* and *Stromatopora bekkeri* have a range of growth form from low to extended domical (text-fig. 9). Such ranges are present in most places sampled, and there is no evidence that they are restricted to low profile forms in particular sites on the biostrome. They are interpreted here as merely younger individuals. Therefore within these specimens, the early stages of growth are low domical, and the V/B ratio increased as the specimen grew, so that its morphology changed from lower to higher domical. Since ragged forms are rare at Kuppen, the taller morphologies are not an artifact generated by sedimentation, as can be the case in stromatoporoids in other environments. Graphs in text-fig. 9 consequently indicate that species adopted either lateral or vertical growth styles, giving low or high profile forms, respectively. These features are summarized in text-fig. 11.

Although the two-fold growth response pattern is clear, there is not as sharp a dichotomy of growth style as this discussion may imply. In text-figs. 9 and 10 a few specimens of *Clathrodictyon convictum*, *Parallelostroma typicum*, *Stromatopora bekkeri* and *Plectostroma intermedium* are large low profile stromatoporoids, which therefore do not fit the pattern. In the field, these stromatoporoids were shown to have more than one growth centre, so that these forms can be accounted for by coalescence of several specimens of one species which happened to grow near each other, and merged as they grew. Coalescence is common amongst conspecifics in stromatoporoids, so presumably there was no immune system response of individuals to members of the same species. Not all coalesced examples became large, low domical forms; cases of extended domical coalesced specimens were found at Kuppen, and the final growth form appears to have been controlled by the number and spatial distribution of conspecifics involved in its generation (text-fig. 11). The same process probably accounts for the larger specimens of *C. mohicanum*, but cannot be recognized satisfactorily in the field because laminae are usually undulose and identification of separate early growth stages is difficult.

Little information is available on morphologies of these stromatoporoids in other localities. Combining information from reports on Silurian stromatoporoids from elsewhere on Gotland, Estonia (Mori 1970; Nestor 1966), Canada (Saville 1979) and New York (Stock 1979), it is clear that morphologies of *Labechia lepida*, *Clathrodictyon convictum*, *C. mohicanum*, *Stromatopora carteri*, *S. bekkeri*, *Lophiostroma schmidtii*, and *Syringostromella borealis* are broadly similar to these species at Kuppen, but several species have also been found with other growth forms. *Ecclinadictyon macrotuberculatum* can be high domical and bulbous in addition to the low domical specimen at Kuppen; *Plexodictyon katriense* is laminar at Kuppen, but domical elsewhere; *Diplostroma yavorskyi* is extended domical as well as the low domical form found at Kuppen; *Plectostroma scaniense* and *Parallelostroma typicum* can be laminar as well as the domical forms at Kuppen. *Stromatopora venukovi* has been reported as domical elsewhere, but at Kuppen there are also laminar forms. These descriptions are not based on comprehensive data, but imply differences in response of these species in other environments.

KUPPEN STROMATOPOROIDS morphology & size

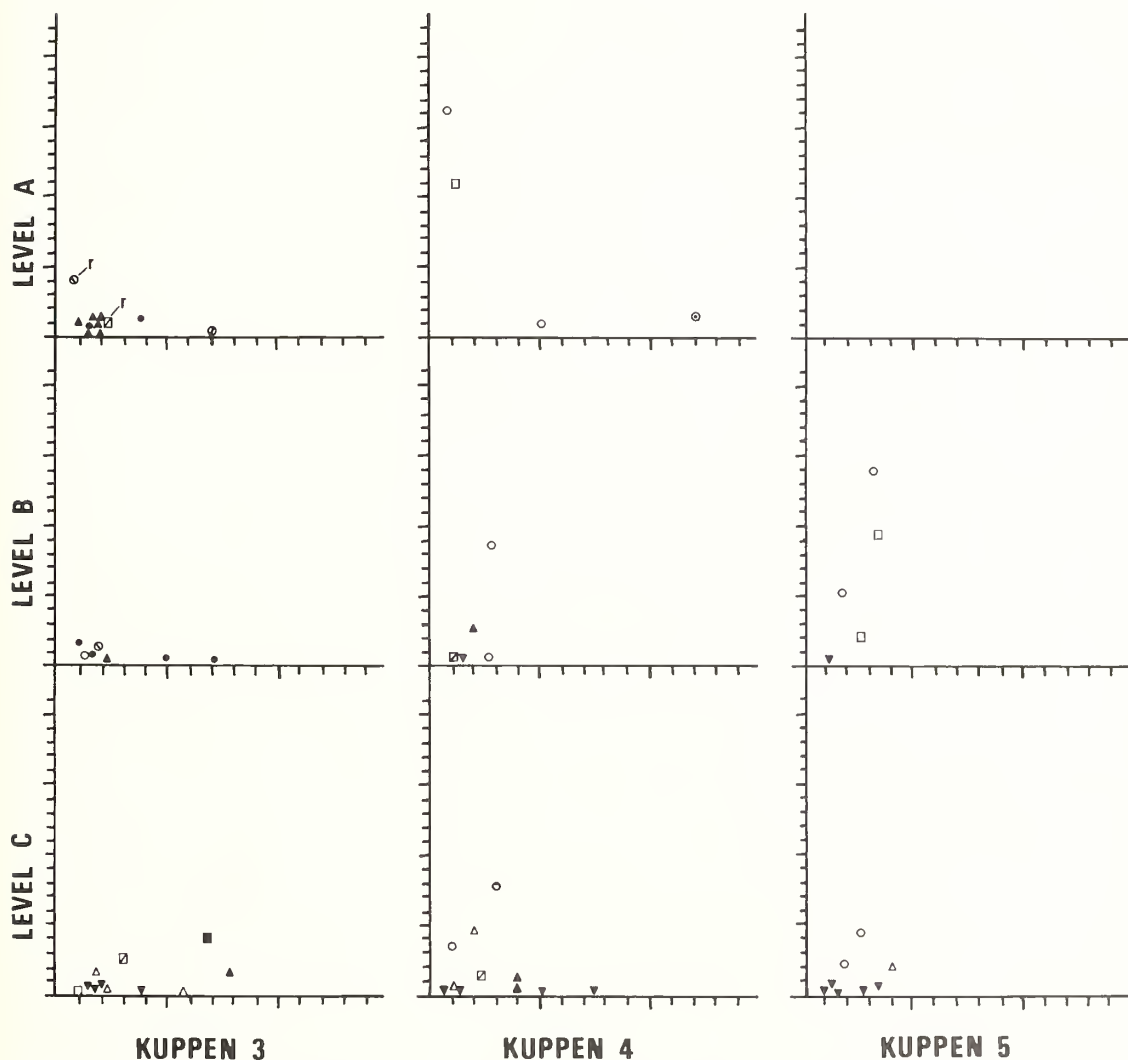
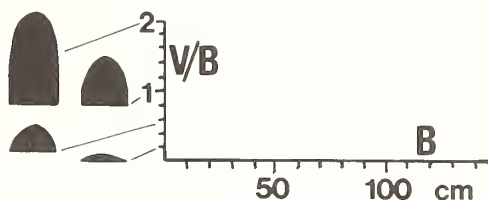
○ <i>S. BEKKERI</i>	22
△ <i>P. INTERMEDIUM</i>	20
• <i>C. MOHICANUM</i>	89
▲ <i>C. CONVICTUM</i>	18



TEXT-FIG. 9. Graphical representation of stromatoporoid morphology, using V/B ratio in relation to basal diameter for the four most common species at Kuppen, arranged according to levels and localities to illustrate abundance and variation in size and morphology. Inset shows scales and morphologies represented by the graphs. Two distinct trends are present, vertical and lateral. See text for discussion.

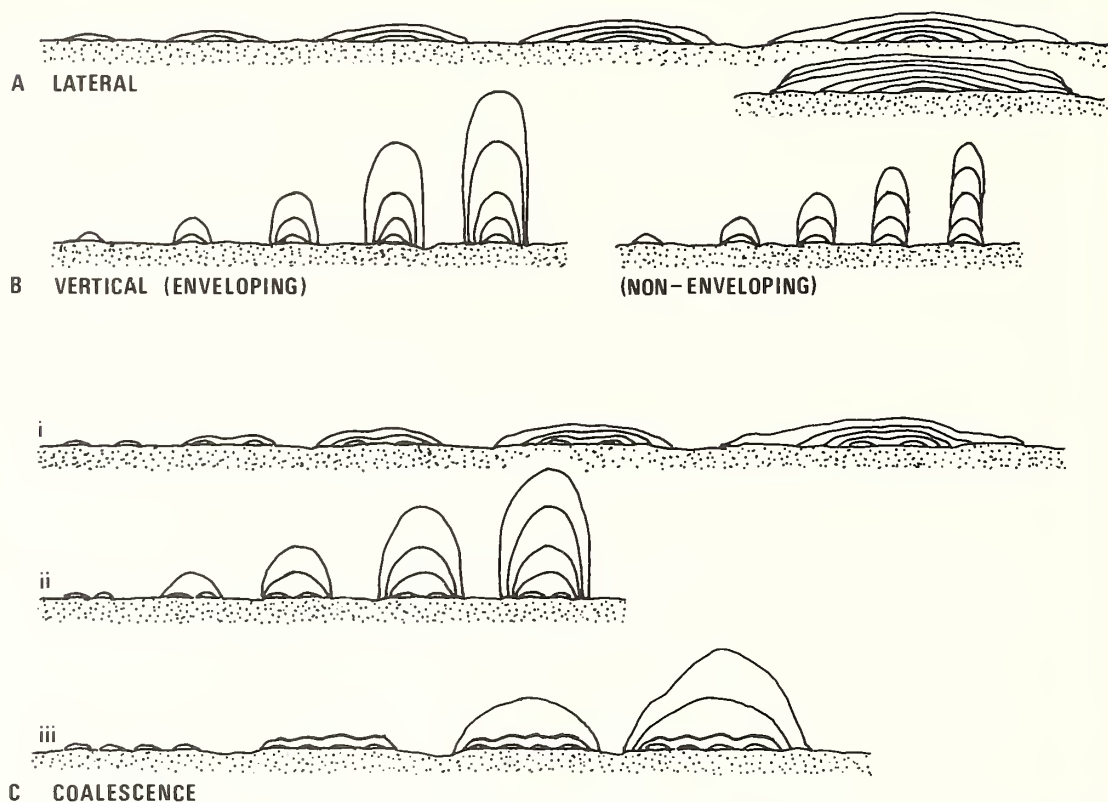
KUPPEN STROMATOPOROIDS morphology & size

• <i>L. LEPIDA</i>	6	■ <i>S. LAMELLOSA</i>	1
⊙ <i>E. MACROTUBERCULATUM</i>	1	▲ <i>S. BOREALIS</i>	11
⊖ <i>P. KATRIENSE</i>	1	△ <i>S. VENUKOVI</i>	6
⊙ <i>D. YAVORSKYI</i>	2	○ <i>P. TYPICUM</i>	11
□ <i>P. SCANIENSE</i>	4	▼ <i>L. SCHMIDTI</i>	15
▣ <i>S. CARTERI</i>	4		



TEXT-FIG. 10. Graphical representation of stromatoporoid morphology, using V/B ratio in relation to basal diameter for the less common species at Kuppen, to illustrate abundance and variation in size and morphology. Inset shows scales and morphologies represented by the graphs.

Kuppen stromatoporoid growth styles



TEXT-FIG. 11. Stromatoporoid growth styles in the lower biostrome, interpreted from text-fig. 9. A. lateral style, developed in low profile forms, such as *Clathrodictyon mohicanum*. B. Vertical style, formed by high profile forms, such as *Plectostroma intermedium*. Many develop enveloping laminae, but others are non-enveloping, while retaining the smooth outline. See text for discussion. C. Forms produced by coalescence of several specimens of the same species which grew near each other. (i) some large low domical forms may be due to this; (ii) high and extended domical forms may contain a small number of early growth stages; (iii) many specimens coalescing may mask the vertical growth style and produce large, low to high domical forms of species which would otherwise be extended domical. Some examples of *Stromatopora beckeri* and *Plectostroma intermedium* in text-fig. 9 are due to this feature.

Morphology of *Plectostroma scaniense* and *Parallelostroma typicum* was examined in more detail by Mori (1970, figs. 23 and 28). His graphs of height plotted against diameter for specimens of these species, in several stratigraphic units on Gotland, reveal considerable variety of morphology and size. Using Mori's data, V/B was calculated, and plotted against B, as in text-figs. 9 and 10. The results are not presented here, but show that, in the Hemse Beds, both species have a range of form from laminar to high domical. Some low profile skeletons are large and may be due to coalescence, although this is not determinable from Mori's data. In the Sundre Beds (upper Ludlow), however, Mori's data show that almost all specimens of both species fall into the low domical field ($V/B = 0.1 - 0.5$), and some large forms are laminar, including a specimen of *Plectostroma scaniense* c. 70 cm in diameter ($= B$). Although Mori's graphs combine data from reef and non-reef localities, Mori (1970, p. 45) noted that stromatoporoid reefs in the Hamra and Sundre Beds are dominated

by low profile forms, and my own field examination revealed a remarkable lack of tall stromatoporoids. Therefore coalescence cannot be responsible for the low profiles, and there is clearly a lateral growth style in these specimens from the Sundre Beds.

STROMATOPOROID DISTRIBUTION AND BIOSTRATINOMY

Stromatoporoid morphology is not uniformly distributed in the biostrome. Visual examination along the length of the outcrop shows that large, low profile forms are most abundant between Snabben 1 and Kuppen 4, but from Kuppen 4 towards Herrvik Harbour such forms decrease in abundance and taller stromatoporoids are more common. Also, the number of stromatoporoids with symbiotic (in the broad sense of the term) syringoporids and rugosans dramatically increases just north of Kuppen 4, and in places is much greater than the 20% average for the biostrome quoted earlier. Sampling the entire length of the biostrome was impractical because of access to the cliff, but the sample sites chosen are clearly representative of the variations present. The only obvious vertical change in the biostrome is that the upper 0.5 m between Kuppen 2 and Kuppen 4 contains stromatoporoids commonly of smaller size, with a more rubbly general appearance than the lower portions.

Text-fig. 6 shows heterogeneity in the vertical and lateral abundance of several species in the biostrome, and analysis of this variation is important to determine palaeoecological characters of the stromatoporoids. The more abundant species show variations as follows. *Lophiostroma schmidtii* and *Stromatopora vemkovi* are present only in the basal part of the biostrome, but in all localities; *Parallelostroma typicum* and *Stromatopora bekkerei* occur throughout (including Kuppen 2; Kershaw 1981) but rarely in the upper portion of the unit; *Syringostromella borealis* occurs only at Kuppen 3 and 4 with more specimens in the upper part; *Stromatopora carteri* also occurs only at Kuppen 3 and 4, but rarely in the upper part; *Plectostroma intermedium* is widespread throughout the biostrome with a lot of fragments at Kuppen 3, and was also found at Kuppen 2 (Kershaw 1981); *Clathrodictyon mohicanum* is abundant everywhere (including Kuppen 2; Kershaw 1981), but diminishes slightly at Kuppen 5; *C. convictum* is more abundant in the lower part, but is missing in Kuppen 3 (one specimen at Kuppen 2; Kershaw 1981); and lastly *Labechia lepida* is uncommon, but is missing from the lower level, and rare at Kuppen 5.

Most laminar to low domical stromatoporoids (e.g. *C. mohicanum*, *Lophiostroma schmidtii* and *Syringostromella borealis*) are complete, upright and probably did not suffer much damage (effects of abrasion have not been recognized because of pressure solution on the stromatoporoid margins). Laminar to low domical forms of all species are usually upright, irrespective of basal diameter. All the species with these morphologies comprise a well developed calcite skeletal structure, with robust laminae and pillars, expected to provide considerable strength to their skeletons. Most of the higher profile species, including *Parallelostroma typicum*, *Stromatopora bekkerei* and *Clathrodictyon convictum*, are also complete, but are commonly overturned (text-fig. 8), and in some cases more damaged than stromatoporoids of lower domical shapes (text-fig. 6). *Plectostroma intermedium* suffered considerable damage in places.

The lack of open reef framework and early cementation permitted ready movement of debris across the biostrome, and this has clearly happened to a substantial number of stromatoporoid fragments. Comparisons of stromatoporoid abundance and growth form between localities can be usefully studied only using complete specimens. Distribution of fragments, however, provides information on severity of damage to stromatoporoids and is a necessary part of ecological study. Since fragments are generally small, around 10 cm across, a large number can be derived from a single stromatoporoid. However, assessment of the number of missing whole stromatoporoids represented by the fragmented material is unrealistic because of the variation in size of complete specimens and of the unknown degree of transport into, and out of, the Kuppen area. Nevertheless, in many species the degree of damage is small, especially in *Clathrodictyon mohicanum*, giving the impression that only a small number of these were broken up during high energy. In the case of *Plectostroma intermedium*, although no broken specimens were recorded in the sampling grid at

Kuppen 5, half the sample there is affected by pressure solution. Its effects distort the relative numbers of complete and broken samples, because most specimens in category s were of small dimensions, and are likely to be fragments; consequently damage to *P. intermedium* is most probably even greater than text-fig. 6 implies. The difference in damage between *C. mohicanum* and *P. intermedium* can be partly attributed to the more easily damaged taller form of the latter, but *P. intermedium* is the most damaged of all the stromatoporoids in the suite and especially so in the upper part of Kuppen 3. The skeleton of this species consists of a network of thin pillars and processes instead of the strong skeleton characteristic of other species with tall forms at Kuppen. Its skeleton appears delicate in thin section and, as has been shown earlier, the majority of cement filling stromatoporoid galleries is dull luminescent, suggesting late (burial) cement. Thus the observed degree of damage is consistent with interpretation of an easily damaged, brittle structure whilst on the sea bed. Consequently the growth forms and skeletal structures of the stromatoporoids possess different preservation potentials. Although most showed non-significant results when using chi-squared tests, comparisons between numbers of specimens of *P. intermedium* and *C. mohicanum* show clearly that the former is significantly more damaged at Kuppen 3 at the 5% level. Chi-squared tests between *P. intermedium* and combined numbers of *Parallelostroma typicum* and *Stromatopora beckeri* showed the same result. This confirms the impression of a delicate structure to *Plectostroma intermedium* compared to the more robust skeletons of *Parallelostroma typicum*-*Stromatopora beckeri*. All these species have similar morphologies (text-fig. 8).

Statistical comparisons are also instructive to assess the general character of the distribution of complete stromatoporoids. Statistical tests were used to compare stromatoporoids between localities, and between levels within localities, but not between levels combined from different localities since level boundaries are arbitrary and no reliable correlation can be made between them. Tests on the distribution of specimens, and of growth forms, show a variety of results. Chi-squared tests were used to compare numbers of complete specimens of pairs of species between localities to determine distributional relationships, and therefore lateral variation. Importantly, *Plectostroma intermedium* increased significantly from Kuppen 4 to Kuppen 5, and over the larger distance from Kuppen 3 to Kuppen 5 when compared with *C. mohicanum* (1% level). *C. convictum* increases significantly from Kuppen 3 to Kuppen 4 in contrast to *C. mohicanum*, and also from Kuppen 3 to Kuppen 5 when tested with *C. mohicanum* and *Syringostromella borealis* at the 5% level. Tests involving *Parallelostroma typicum* and *Stromatopora beckeri* were considered unreliable in view of taxonomic problems and were omitted. Tests using other species were not particularly informative in view of the small numbers, although much variation in distribution is evident from Table 1 and text-fig. 6.

The above tests illustrate large scale lateral changes, but variations can be recognized between levels within localities. Thus each level is considered to be time-averaged and compared as a unit with other levels to illustrate temporal changes in the development of the stromatoporoids at any site. With use of the Fisher exact probability test, the visual decrease in basal diameter (a measure of size) of *C. mohicanum* from Kuppen 3B to 3A (text-fig. 9) is significant only at the 13% level, and the increase from 4B to 4A at the 9% level. With levels combined to compare localities, the visual reduction in size from Kuppen 4 to 5 reveals significance at the 11% level. These results are therefore not regarded as significantly different. The Fisher test also reveals a non-significant result when the V/B ratio (a measure of shape) in *Plectostroma intermedium* is compared between Kuppen 4 and 5 ($P = 0.48$) and when Kuppen 5 is compared to both Kuppen 3 and 4 combined ($P = 0.24$). Thus specimens of this species are not significantly taller at Kuppen 5 than at Kuppen 4 or Kuppen 3, as might be expected in the quieter environment of Kuppen 5.

To summarize important features of the tests: *C. mohicanum* (a low profile form) is significantly less abundant at Kuppen 5 compared with *Plectostroma intermedium* (a tall profile form), which increases sharply at Kuppen 5; *C. mohicanum* varies in size between levels and localities, but not significantly, and some less abundant species show fluctuations in abundance laterally in the biostrome. It can be argued that the striking difference in distribution of numbers of whole samples of *C. mohicanum* and *P. intermedium* is an artifact caused by extensive damage to *P. intermedium*

at Kuppen 3A. However, it should be noted that the number of whole specimens of *P. intermedium* which would need to have been destroyed to generate the fragments is relatively small, because debris is much smaller than whole specimens, even if the stylolitized samples (most of which were probably originally fragments) are included. Also, no fragments of *C. mohicanum* were collected from Kuppen 3A, and the complete specimens were of smaller size than in most other sites (text-fig. 9). Other species with a variety of growth profiles are represented largely by complete specimens in Kuppen 3A (Table 1), and the overall impression is of localized movement of debris. Variations in distribution of stromatoporoid species vertically and laterally throughout the biostrome support this (text-fig. 6 and Table 1) and reflect the life distribution of the stromatoporoids, thus broadly relating to their palaeobiology.

Lastly, a curious feature of the Kuppen stromatoporoids is a notable lack of bioerosion. Stromatoporoids from the Upper Visby Beds (lower Wenlock, Gotland), for example, are heavily bored by *Trypanites*, but not at Kuppen. Thus the damage to stromatoporoids at Kuppen can be safely attributed to physical processes.

CONTROLS ON STROMATOPOROID GROWTH

The very high abundance of stromatoporoids in the biostrome was an important aid to the development of its fauna, because of the provision by taphonomic processes of a substrate of dead skeletons of earlier individuals. Particularly significant is the dominance of low profile stromatoporoids. *C. mohicanum* must have acted as a key substrate stabilizer, and *Lophiostroma schmidti*, with its characteristic encrusting habit, would have assisted in immobilizing areas of substrate. Some specimens of this latter species are large (text-fig. 10), and occur in the lower portion of the biostrome as well as in the marl beneath. In the absence of a cemented frame, the stability of laminar and low domical stromatoporoids in a regime of low sedimentation, allowed repeated colonization of the surface. Encrusting crinoids, bryozoans, and rugose and tabulate corals have also made use of this facility. *L. schmidti* was also commonly found encrusting, and was encrusted by, other stromatoporoid species, a feature noted by Mori (1970).

Distributions of species in the lower biostrome are clearly heterogeneous. The south end of the Kuppen complex shows coarser grained sediments overlying the biostrome, and deep palaeo-erosion into it. The northwestern end (at Kuppen 5) shows a thinning of the unit and frequent interfingering of sediment in the area between Kuppen 5 and Herrvik. Lower energy water permitting a higher sedimentation rate in the Kuppen 5 area would have selected taller forms, and prejudiced survival of low profile stromatoporoids because of greater chance of them being buried. This could account for the distributional differences between *P. intermedium* and *C. mohicanum*, but paucity of ragged forms implies an overall low depositional rate. Most specimens of *Clathrodictyon convictan* show a smooth non-enveloping form, suited to a lower energy situation with an increased sedimentation rate at Kuppen 5, so that growth was concentrated at the apex of individual stromatoporoids. The small numbers and size of *C. mohicanum* at Kuppen 5 could be taken to indicate inhibition of growth by slow continuous sedimentation, rather than periodic deposition which would have led to development of ragged forms.

Species-morphology relationships in the Kuppen suite show a pronounced taxonomic control on growth form (text-figs. 8–10), and illustrate ontogenetic patterns in growth form development (text-fig. 11). The reasons why different species developed different growth forms, however, remain undiscovered. While sedimentation rate is invoked here to play a part in controlling distribution, the abundance of low profile forms and rarity of ragged shapes indicates an overall low rate of deposition for the biostrome, and therefore sedimentation cannot be inherently responsible for the differences in form. In conditions of low energy, some species may have grown upwards to create local turbulence as suggested by Kershaw (1981). This speculative point could be invoked to explain why tall forms grew in the NW area, but since high and low profile forms occur upright and in close proximity in the southern area at Kuppen 2 (Kershaw 1981) and can be satisfactorily regarded as being *in situ*, such an interpretation cannot be generally applied. Also, apart from those at the base

of the biostrome, there was no need for low profile forms to develop as a response to avoid sinking in soft sediment, because their substrate was mostly dead skeletons of stromatoporoids, suitable also for taller forms because of the stability of a hard surface.

Work on Devonian stromatoporoids illustrates the importance of lateral growth as a competitive feature (Meyer 1981), which would account for the abundance of *C. mohicanum*. However, competition for space between stromatoporoids at Kuppen, whereby fast growing, low profile forms would have commanded large areas of substrate, forcing others to grow upwards, cannot explain the dichotomy of form because of the different distributions of *Plectostroma intermedium* and *Clathrodictyon mohicanum* (text-fig. 6). Abundance of low profile shapes could be related to a competitive feature, but also to adaptation to an occasionally turbulent environment with storm action selectivity removing taller forms periodically. Since energy was lower most of the time, a low profile shape would only be necessary for that purpose in times of high energy.

Recent work on other stromatoporoid assemblages also indicates the selective advantage of lateral growth. Harrington (1987) describes the usefulness of a lateral growth habit for colonizing unstable substrates in Devonian stromatoporoids. Bjerstedt and Feldmann (1985) show how stromatoporoid morphology varies from stabilizing, low profile forms in the lower parts of a Middle Devonian reef to more erect shapes once stabilization has been achieved. Therefore the development of a low profile form can be explained in a number of ways, with difficulty in distinguishing between them. Thus at Kuppen the presence of higher profile forms could be attributed to fluctuations of environmental energy, allowing periodic colonization by stromatoporoids with high profile shapes which were selectively damaged during storms.

Stromatoporoids which normally formed tall shapes are occasionally large, low domical morphologies (text-fig. 9). These are demonstrably due to coalescence of several individuals, and the simultaneous growth of a number of stromatoporoids near each other is circumstantial evidence for growth on dead areas of substrate since closely packed fossils were not necessarily alive simultaneously. In the case of *Stromatopora bekkeri* (text-fig. 9), the location of these particular specimens at the base of the biostrome at Kuppen 3 is also notable, their substrate being the underlying bedded marls (text-fig. 2) poorly populated by stromatoporoids. Development of a low profile form in this situation would also help to spread weight on a soft substrate. Kershaw (1984) suggested substrate control for low profile forms in the Upper Visby Beds (Wenlock) on Gotland.

Data presented by Mori (1970), noted earlier, show that stromatoporoid reefs in the Sundre Beds are dominated by low profile stromatoporoids. This reinforces the importance of a low profile in reef-builders. The principal species in these Sundre reefs, *Plectostroma scaniense* and *Parallelostroma typicum*, are tall forms at Kuppen, while the dominant stromatoporoid at Kuppen, *Clathrodictyon mohicanum*, is missing from the Sundre Beds (upper Ludlow, younger than the Hemse Beds). There is clearly a need to investigate the reasons for these differences, which may involve environmental changes, selecting for some species and excluding others. However, the possibility of adaptive evolution towards a more efficient growth form in some species also needs to be considered.

Stromatoporoid growth irregularities

Some stromatoporoids at Kuppen exhibit small protrusions, called mamelons, 0.5–2 cm in height, and not associated with astrorhizae as mamelons sometimes are. They occur rarely in *Stromatopora bekkeri*, *Parallelostroma typicum*, *Plectostroma scaniense*, and *P. intermedium*, but they covered the upper surface of the skeleton in 7 of the 107 specimens of *C. mohicanum*. They were vertically orientated in specimens which lay with their basal dimension horizontally on the substrate, but one specimen lying at an angle of c. 30° from horizontal in the upper part of Kuppen 3 still had vertically orientated protrusions (text-fig. 7). This latter feature was also found in several unidentified stromatoporoids from other parts of the biostrome and a recrystallized stromatoporoid from a biostrome in the Klinteberg Beds at locality Vivungs 1 of Laufeld (1974a), and lead to speculation as to their cause.

Boyajian and La Barbera (1987) investigated mamelons experimentally in conjunction with astrorhizae in model stromatoporoids and *Ceratoporella nicholsoni* and showed their importance in

directing water currents through the structure to maximize feeding. This work is based on the well established Bernoulli's principle of water flow from high pressure, slow moving water near the stromatoporoid skeleton to low pressure faster moving water around the tips of protrusions (Vogel 1978).

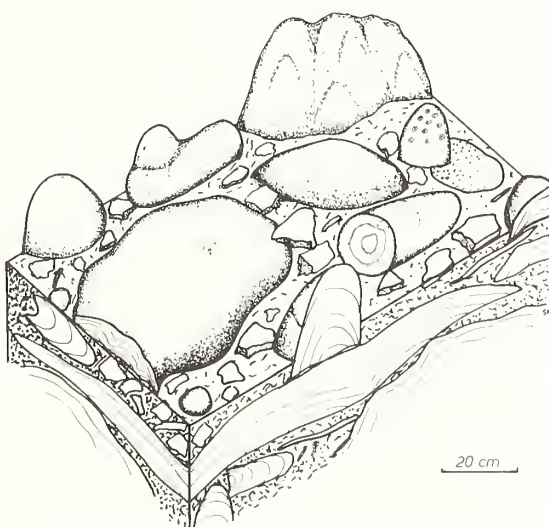
Mamelons in the present specimens could have had a similar function, or as Kershaw (1981) suggested, caused turbulence close to the skeleton surface to assist feeding. The absence of astrorhizae on surfaces of many stromatoporoids does not necessarily negate a relationship with water flow, because in many modern calcified sponges the astrorhizal system exists entirely in the soft tissue coat and makes no impression on the skeleton. Nevertheless, in many stromatoporoids at Kuppen, and elsewhere in Silurian and Devonian rocks, there is a calcified astrorhizal system that is not associated with mamelons, and so the importance of mamelons in controlling water currents is questionable. Also, the presence of vertically orientated mamelons on sloping stromatoporoids suggest that other factors are responsible for mamelon development.

Suggestions have been made that stromatoporoids were photoresponsive. Kazmierczak (1969) proposed symbiotic ?algae, and also that stromatoporoids are themselves cyanobacteria (e.g. Kazmierczak and Krumbein 1983). Since only a few specimens of *C. mohicanum* have such protrusions, they are unlikely to represent a photoresponse in this case. Surface morphology of the biostrome was suggested by Kershaw (1981) to cause mamelon growth in hollows. Although surface depressions on the biostrome are not identifiable due to biostatinomic effects, their inferred presence could explain the specimens with mamelons. They are present in several localities and levels and consequently not limited to particular parts of the biostrome. They could therefore be a response to low energy causing an increase in stromatoporoid surface area and enhanced eddy formation for feeding in quiet spots. However, they cannot reflect increased sedimentation where they occur since the 'valleys' between mamelons only rarely contain sediment, and laminae of the stromatoporoid are continuous over the tops of mamelons and the valleys between them.

CONCLUSIONS

This study reveals two major growth styles in stromatoporoids in a low diversity assemblage, favoured by one species, in a low to moderately turbulent environment with a low sedimentation rate. Environmental gradients involving water turbulence and sedimentation appear to have played an important role in controlling distributions of species and growth forms. The abundance of low

TEXT-FIG. 12. Reconstruction of a small part of the lower biostrome, showing many stromatoporoids in life attitude, and taller forms overturned, plus fragments. Large, low profile shapes are based on *Clathrodictyon mohicanum*, and taller forms on *Plectostroma intermedium*. One specimen contains rugose corals, while an extended domical form on its side has continued to grow following overturning. A large domical form has developed by coalescence. Matrix is micrite, with skeletal debris.



profile stromatoporoids, in particular *Clathrodictyon mohicanum*, can be attributed to a number of factors including substrate colonization, stability of the substrate during times of higher energy, competitive ability, and coalescence, and is favoured by a low sedimentation rate. Most stromatoporoids in the suite grew on dead skeletal material, providing an important feedback to the living assemblage. Biostratinomic movement of skeletons, selective removal of taller growth forms and the pervasive effects of pressure solution, have distorted the life assemblage. A composite reconstruction of a small area of typical biostrome surface is shown in text-fig. 12, to illustrate the biostrome surface at an unspecified point in its development.

Acknowledgements. I gratefully acknowledge funding from the West London Institute, with additional support from the Swedish Geological Survey, and access to the Allekvia Field Station on Gotland. I thank Robert Riding (Cardiff, U.K.), Michael Keeling, Julian Harrigan and Nicholas Palaus (West London Institute) for discussions on the Kuppen Complex, and Peter Sutcliffe (Kingston Polytechnic, U.K.) for assistance with cathodoluminescence. I am grateful to Colin Stearn (McGill, Canada), Michael Bassett (National Museum of Wales, U.K.) and reviewers for many helpful comments in the manuscript. This work is dedicated to Ruth and Reginald Kershaw.

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Typescript received 7 March 1989

Revised typescript received 20 December 1989

REVIEW OF THE CAENOZOIC HETERODONT BIVALVE SUPERFAMILY DREISSENACEA

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ABSTRACT. The Dreissenacea consists of one family, the Dreissenidae, with subfamilies Dreisseninae for *Dreissena* (with three subgenera), *Congeria* and *Mytilopsis*; and Dreissenomyinae for *Dreissenomya* (two subgenera). Poorly preserved *Prodreissensia* is provisionally placed in the Dreisseninae, but may be wrongly assigned to the superfamily. Dreissenids live in fresh and brackish water. Most are epifaunal and byssally attached but *Dreissenomya* was infaunal and unattached. *Mytilopsis* first appeared in the European Eocene and invaded the Western Hemisphere in the late Oligocene. *Dreissena*, *Congeria* and *Dreissenomya* arose in the late Miocene of the Paratethys. Two genera survive: *Mytilopsis* occurs naturally only in the Western Hemisphere and *Dreissena* in Europe and Western Asia. European Mio-Pliocene boundary extinctions coincide with the break up of Paratethys and the Messinian salinity crisis. Often anomalous increases in the distribution of both Recent genera are attributed to human activity, but some records from eastern Asia are due to confusion with *Sinomytilus* (Mytilacea).

THE largely freshwater, eulamellibranchiate, anisomyarian superfamily Dreissenacea first appears in the Eocene and is still living. It was placed in the Veneroida (Heterodonta) in the classification of Newell (1965) which was adopted by McCormick and Moore *in* Moore (1969). Confirmation of this position was provided by Taylor, Kennedy and Hall (1973) who stressed the strong resemblance between the shell structures of *Dreissena* itself and the Corbiculacea, another largely freshwater superfamily which dates back into the Mesozoic.

Examination of the fossil record and the Recent distribution of the Dreissenacea shows that the generic ranges, geographical distribution and arrangement of the genera given by Keen *in* Moore (1969) (see Table 1) in the Treatise and by Eames *in* Morley Davies (1971) are in need of modification. The Treatise classification (Moore 1969) had some influence on the views of both Morton (1970) and Marelli and Gray (1985) on evolution the superfamily: in consequence, several of their conclusions also need re-examination.

It is understandable how much of the confusion arose. Firstly for generic determination it is necessary to examine internal features of the shell: one such feature is the presence or absence (pl. 1, figs. 6, 14, 16) of the apophysis which may be hidden under the septum and can easily be overlooked except in good specimens and good illustrations. Secondly, many species were originally described either as *Mytilus* or *Dreissena*. In addition, this situation is further complicated by the almost universal practice of European workers of placing all species possessing an apophysis in *Congeria*, regardless of the fact that most resemble the type species of *Mytilopsis* (pl. 1, figs. 11–14) rather than that of *Congeria* (pl. 3). Thirdly, it is becoming clear that many Recent occurrences of both *Dreissena* and *Mytilopsis* are the result of human introduction.

Oppenheim (1891, pl. 51) gave excellent illustrations of the internal details of several European Eocene species, showing that all whose internal features were known possessed an apophysis (pl. 2, figs. 12–18). These species had been originally described as *Dreissena* and have subsequently been assigned to various subgenera of *Congeria*, but are here regarded as belonging to *Mytilopsis*. Most subsequent European studies, however, have concentrated on the varied dreissenid faunas of the Neogene of the Paratethys, stretching from Austria eastwards through the southern USSR as far as the Aral Sea. The basis of the more recent Russian classifications (Starabogatov 1970; Babak 1983) is the work of Andrussov (1897–8; 1900) whose very comprehensive monograph of fossil and

TABLE 1. Summary of modern classifications of the Dreissenacea

Keen <i>in</i> Moore (1969)	Babak (1983)	Herein
Fam. DREISSENIDAE	Fam. DREISSENIDAE	Fam. DREISSENIDAE
	Subfam. DREISSENINAE	Subfam. DREISSENINAE
<i>Dreissena</i> (<i>Dreissena</i>)	<i>Dreissena</i> (<i>Dreissena</i>)	<i>Dreissena</i> (<i>Dreissena</i>)
—	(<i>Pontodreissena</i>)	(<i>Pontodreissena</i>)
—	(<i>Modiolodreissena</i>)	(<i>Modiolodreissena</i>)
(<i>Prodreissensia</i>)	—	<i>Prodreissensia</i>
<i>Dreissenomya</i> (<i>Sinucongeria</i>)	—	
<i>Congeria</i>	<i>Congeria</i> (<i>Congeria</i>)	<i>Congeria</i> (= <i>Congeria</i>)
	(<i>Rhombocongeria</i>)	(= <i>Congeria</i>)
	(<i>Eocongeria</i>)	(= <i>Mytilopsis</i>)
	(<i>Trigonipraxis</i>)	(= <i>Mytilopsis</i>)
	(<i>Andrusoviconcha</i>)	(= <i>Mytilopsis</i>)
<i>Mytilopsis</i>	(<i>Mytilopsis</i>)	<i>Mytilopsis</i>
	Subfam. DREISSENNOMYINAE	Subfam. DREISSENNOMYINAE
	<i>Dreissenomya</i> (<i>Dreissenomya</i>)	<i>Dreissenomya</i> (<i>Dreissenomya</i>)
	(<i>Sinucongeria</i>)	(<i>Sinucongeria</i>)

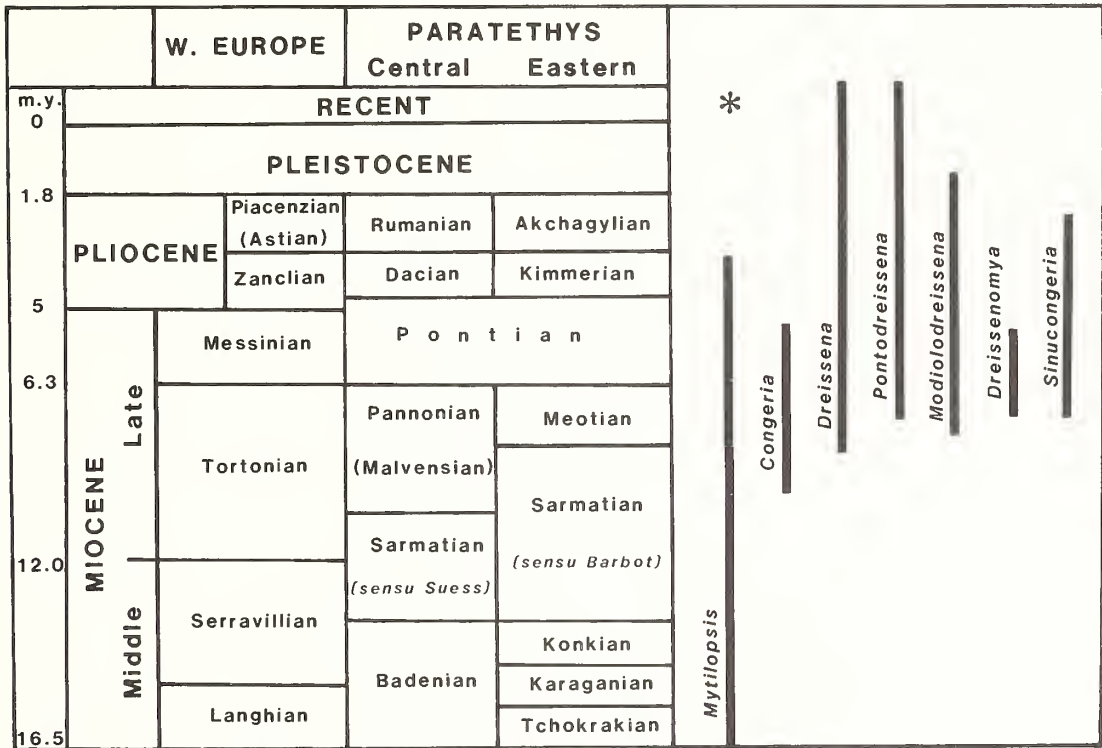
TABLE 2. Relationship between informal groups of the genus *Congeria* proposed by Andrussov (1897–8) and the subgeneric arrangements adopted by Starabogatov (1970) and Marinescu (1973)

Andrussov, 1897–8*	Starabogatov, 1970	Marinescu, 1973
eocenae <i>eocena</i> (sic) = <i>eocenica</i> Oppenheim	<i>Eocongeria</i> nov. subgen.	—
mytiliformes <i>basteroti</i> Deshayes	<i>Mytilopsis</i> Conrad	<i>Mytilia</i> nov. subgen.
modioliformes <i>amygdaloides</i> Dunker	<i>Andrusoviconcha</i> nov. subgen.	<i>Modiola</i> nov. subgen.
subglobosae <i>no type species</i>	<i>Congeria</i> Partsch	<i>Congeria</i> Partsch
rhomboidea <i>no type species</i>	<i>Rhombocongeria</i> nov. subgen.	<i>Rhomboidea</i> nov. subgen.
triangulares <i>triangularis</i> Partsch	<i>Trigonipraxis</i> nov. subgen.	<i>Triangularia</i> nov. subgen.

* Andrussov's informal groups and their 'type species' are shown in this column.

living Dreissenidae of Eurasia also dealt with species from the rest of the world. Andrussov (1898) divided both *Congeria* and *Dreissena* into a number of non-binomial 'groups', and gave 'type species' for some but not all of them (see Table 2). Later authors have subsequently formalized these groups as nomenclatorially valid subgenera, sometimes with type species different to those originally suggested by Andrussov. In the present work all such subgenera of *Congeria* are

synonymized either with *Conger* or *Mytilopsis* (Table 1). The aim of the present study is to revise the stratigraphic and geographic distributions of the various genera and to suggest improvements to the classification adopted by earlier authors. Text-fig. 1 shows the correlation adopted herein for the European post-Lower Miocene.



TEXT-FIG. 1. European post-lower Miocene correlation and generic ranges. *Mytilopsis* first occurs in the Eocene. Key, asterisk, *Mytilopsis* reintroduced after becoming extinct in eastern Hemisphere. Based on Steininger *et al.*, 1985.

The generic synonymies given herein concentrate on names proposed in modern taxonomic works. They omit the numerous variations in the spelling of *Dreissena*. Also omitted are the many nineteenth-century names which have long since fallen into disuse. This information is readily available elsewhere (Keen *in* Moore, 1969; Vokes 1980).

The scope of this study is somewhat limited by the comparatively small collections in the Palaeontology and Zoology departments, British Museum (Natural History) (BMPD; BMZD) and is therefore largely based on reinterpretation of the literature. Probably the most useful source of reliable specific identifications and natural groupings is Andrussov (1897-8). Other important works consulted include the following concerned with classification: Orlov (1960); Keen *in* Moore (1969); Starabogatov (1970); Babak 1983.

Works summarizing regional distribution and containing illustrations and references sufficiently adequate for reinterpretation include: for Europe:- Archambault-Guezou (1976a, b); Iljina *et al.* (1976); Locard (1893); Marinescu (1973, 1975); Oppenheim (1891, 1892); Papp (1953, 1954); Rozanov (1986); Zelinskaya *et al.* (1968); for the Western Hemisphere:- Keen (1971); Marelli and Gray (1983); Olsson (1961); Nuttall (1990, pp. 275-287); for West Africa:- Pilsbry and Becquaert (1927). Anatomy and other aspects of the biology of living *Dreissena* are dealt with by Morton (1970) and by Yonge and Campbell (1968). Escarbassiere and Almeida (1976) and Morton (1981)

dealt similarly with living *Mytilopsis*. Several, mainly early, papers have been largely ignored because it is not possible to interpret the sparse stratigraphical information they contain. For example, among those that have proved too difficult to use is the important study of Yugoslav Miocene dreissenids by Kochansky-Devidé and Slisković (1978). They figured many apparently rather crushed species and introduced (pp. 35, 60) a new informal group, the 'luciniiformes'. Their range chart (p. 76) differs from current views in correlating the Tortonian with the Badenian, regarding both as pre-Sarmatian. They placed both the Otnangian and Karpathian within the Helvetian, which they regarded as pre-Badenian. Nowadays the general consensus is to consider the Helvetian as equivalent to the Tortonian.

MORPHOLOGY AND MODE OF LIFE

Inequivalvity

Slight inequivalvity in the Dreissenacea arises from two factors. In all genera except *Dreissenomya*, some articulation, or rather means of relative location between the two valves, is achieved by differences in the ventral shell margin or commissure immediately posterior to the umbones (pl. 1, figs. 2, 3). In the left valve a sinus followed by a broader upswelling is developed just posterior to the umbo. In *Dreissena* (*Pontodreissena*) *rostriformis* (Deshayes 1838) upswelling is very pronounced, forming a strong beak (pl. 1, figs. 8–10). In the right valve, an upward angular projection is present immediately posterior to the umbo. The sinus developed behind this projection is rather weaker than the upswelling in the left view. These structures, which are purely modifications of the commissure, are not true hinge teeth, even though they are concerned with articulation. The other cause of inequivalvity is that the byssal notch is not always developed evenly in both valves. Yonge and Campbell (1968, p. 5) stated that in *Dreissena polymorpha* (Pallas) the umbo of one valve overlaps that of the other ventrally, and this one alone bears the byssal notch. They did not state which valve is which and their observation on the byssal notch cannot be confirmed. This species lives in clusters with the result that both shell shape and also the orientation of the byssal anchorage could well be influenced by crowding against adjacent shells. This habit of living in tight clumps adopted by most dreissenids (text-figs 2A, E) can cause considerable morphological variation due to pressure from adjacent individuals. This has led to the description of numerous unnecessary nominal species, as witnessed by the lengthy synonymies in Marelli and Gray (1983) and in Nuttall (1990, pp. 280, 285) of, respectively, Recent and Neogene *Mytilopsis*. Similar reservations must be expressed about the large number of other fossil species described as occurring either together or at particular horizons. Internal inequivalvity may occur in the septal region. The septa of the two valves are often not mirror-images of each other. Variations occur in the size and shape of the muscle attachments on the septa and also the way in which the septa may, or may not be, supported or buttressed from below.

Anterior muscle attachments

The form of the septum and its muscle attachments have provided the basis not only of generic separation but also much of the evidence of the evolution of the family. The anterior adductor muscle is always attached to the septum. In *Dreissena* (pl. 1, fig. 6) and *Dreissenomya* (pls. 5, 6; text-fig. 3) the pedal/byssal retractor scar occurs on the dorsal part of the septum. In *Mytilopsis* (pl. 1, figs. 14, 16) the pedal/byssal retractor scar is situated on a myophore placed sometimes slightly underneath, sometimes posterior to, the dorsal part of the septum. In *Congeria* (s.s.) this myophore tends to be fused to the dorsal margin of the septum (pl. 3). This fusion may be interpreted as resulting from massive thickening of the septum rather than a fundamental difference between *Congeria* and *Mytilopsis*. The taxonomic usefulness of the septum and apophysis has been questioned (Archambault-Guezou 1982, with further references). Previously (1976a, pl. 9, figs. 16, 17) she had illustrated juvenile valves of the southern French 'infra-Pliocene' (= Messinian) '*Congeria*' *rhodanica* (Fontannes 1882) (here transferred to *Mytilopsis*). In the right valve the

apophysis is fused to the septum and the pedal/byssal scar is deep and oval. In the left valve the apophysis is mounted behind and below the septum.

Archambault-Guezou (1976b) was clearly of the opinion that '*C. rhodanica*' was extremely closely related to '*C. subcarinata*' (Deshayes 1838) originally described from the Pliocene of the Crimea. Morton (1970) figured a left valve (BMPD LL18540) of '*C. subcarinata botenica*' Andrussov, 1897 from the Middle Pontian of Rumania in which the apophysis is fused to the septum. Examination of a further sample (BMPD LL9022-4) from another Rumanian locality of Upper Pontian age (pl. 6, figs. 8-10) confirms his observation on the left valve, but also shows that the apophysis in two accompanying right valves is in the normal position for *Mytilopsis*. This is a mirror image of the situation in *M. rhodanica*. Unfortunately, lack of material makes it impossible to discover how constant the difference between valves is in these two species or subspecies. The possibility that the difference is random, caused by the shells living at different attitudes in clumps, cannot be dismissed.

Examples of reduction of the apophysis in apparently different lineages during the late Miocene are illustrated by Papp (1950) and Pana (1962). This suggests that *Dreissena* may be polyphyletic and is, perhaps, some justification for the recognition of its three described subgenera.

All these aberrations in the arrangement of the septum and apophysis are perhaps to be expected at a period during which the Dreissenacea were evolving rapidly. If *Mytilopsis* gave rise to *Congeria* and *Dreissena*, it seems highly likely that the quite good fossil record should reveal fossils, such as those discussed above, which may be interpreted as intermediate forms. I will accept, therefore, the presence of the apophysis, or lack of it, as being a useful taxonomic distinction in most instances. Morton (1981, p. 39), in discussing the anterior pedal retractor in *Dreissena*, *Congeria* and *Mytilopsis*, inferred that the introduction of the apophysis was a progressive improvement, and his fig. 11 certainly supports his view that there is an increase in the mechanical efficiency of the pedal/byssal retractor muscle. It is, however, a reverse of the evolutionary sequence. *Mytilopsis*, with an apophysis, appeared some 40 million years before *Dreissena* dispensed with this structure, and is still successful.

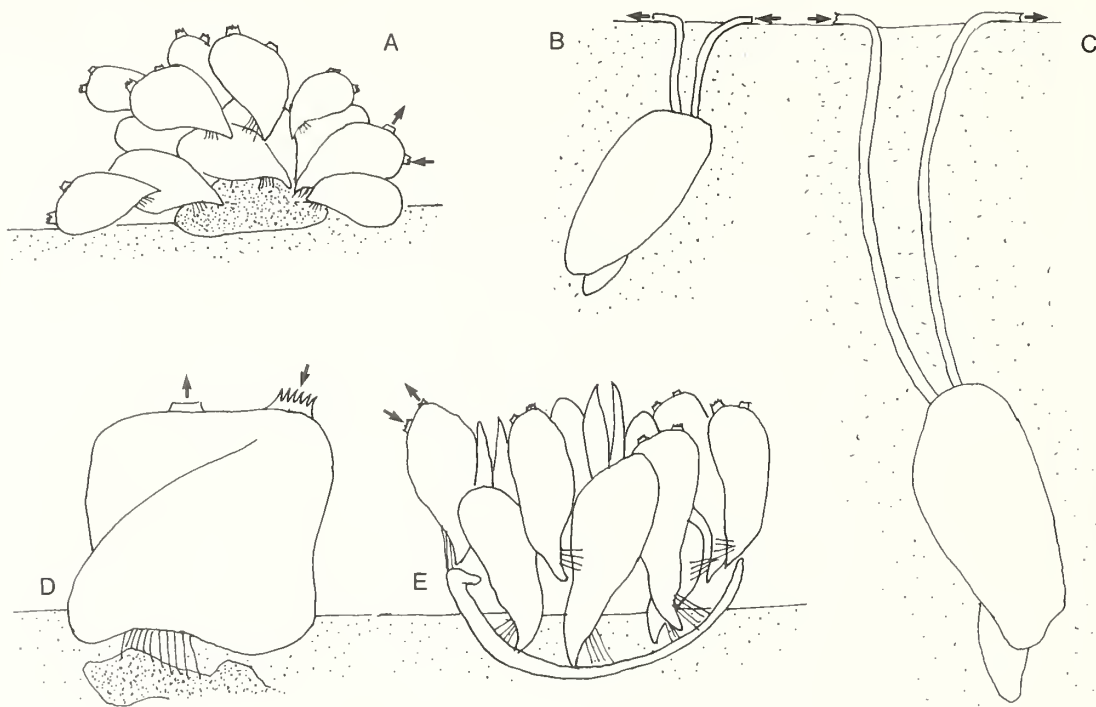
Articulation

The family appears to be edentulous. Morton (1970) described and figured the interiors of left valves of *Dreissenomya* (*Sinucongeria*) *aperta* (Deshayes 1838) (BMPD LL18541) and *Congeria* (*C.*) *subglobosa* Partsch (BMPD LL22134), stating that the former has two rudimentary cardinal teeth and the latter a poorly developed cardinal covered in life by the anterior adductor. In fact, both valves of LL18541 possess a single irregular rugose ridge crossing the hinge plate (pl. 6, figs. 1, 2, 5, 6). These ridges, however, are not only far too low to articulate as teeth, but are also in the wrong position to do so. They are situated more or less opposite each other rather than being offset like true teeth which fit into corresponding sockets in the other valve. Another specimen (BMPD L19502; pl. 6, figs. 3, 4, 7) and numerous illustrations (Archambault-Guezou 1976a, pls. 4, 5; Marinescu 1975, pls. 6-8) show wide variation in both size and position of these ridges on the septum of *D. (S.) aperta*. Similar ridges occur in other species of *Sinucongeria*. Examination of LL22134 and other specimens of *Congeria subglobosa* (Pl. 3) shows that no cardinal tooth, however poorly developed, exists. The ridge is not always present, and, as in *Sinucongeria*, cannot have acted as a tooth. These ridges are here interpreted, therefore, as some modification to the adductor muscle attachment area rather than as rudimentary dentition. It is possible that they mark the boundary between the 'catch' and 'quick' components of the anterior adductor muscle. Yonge and Campbell (1968), however, in rather briefly discussing the musculature of *Dreissena polymorpha* (Pallas), do not mention finding these two separate components of the adductor muscle. An alternative explanation is that ridges or corrugations might help to make a more secure anchorage between the muscle and shell.

Marinescu (1975, p. 78, text-figs. 4, 5, 6, 8) stated that there was a rudimentary cardinal tooth in the right valve of *Dreissenomya* (s.s.), in contrast to *D. (Sinucongeria)*, which he described as edentulous. His text-fig. 5 illustrates a series of juvenile shells (0.6-1.3 mm long). The structure,

situated on the commissure just below the umbo, is in the correct position for a tooth, but (his text-fig. 5E) also occurs in the left valve. In adult shells (BMPD L19501, L71745) (pl. 5, figs. 1–5) it appears to match a slight indentation of the commissure below the umbo, and is unlikely to have been an effective form of articulation. This structure could be equivalent to the flexures of the commissure in the umbonal region of more typical members of the family, rather than a cardinal tooth.

The umbones are terminal in the majority of Dreissenacea, including the earliest known. It is only in the late Tertiary *Dreissenomya* (s.s.) that they are situated some distance behind the anterior of the shell, but still well forward. The change in umbonal position can be regarded as a secondary modification connected with adaptation to an epifaunal mode of life (text-fig. 2B, C).



TEXT-FIG. 2. Mode of life of Dreissenacea. Arrows indicate inhalent and exhalent siphons. A, Recent *Dreissena* and *Mytilopsis*, epifaunal, byssally attached to hard object such as pebble or piece of wood. Dead shells at bases of cluster shown without siphons. B, extinct *Dreissenomya* (*Simucongeria*) and C, *D. (Dreissenomya)*, both infaunal, powerful burrowers, with foot extended. D, extinct *Congeria subglobosa* Partsch, epifaunal, attached to hard object by massive byssus. E, extinct *Mytilopsis spathulata* (Partsch) epifaunal, byssally attached cluster on dead valve of *Congeria subglobosa*, dead shells shown without siphons, or with valves not closed. Based on LL 28243. Upper Miocene, Pannonian, Hennesdorf Brick Pit, 10 km S. of Vienna. All extinct examples from late Miocene and Pliocene of Paratethys. B and C modified from Marinescu, 1975. All figures approximately $\times 0.5$.

Mode of life

All known Recent species of both *Dreissena* and *Mytilopsis* are epifaunal, living in clusters attached to each other by the byssus (text-fig. 2A). The cluster or colony (text-fig. 2E, BMPD LL28243) of the Austrian Pannonian *Mytilopsis spathulata* (Partsch) on a single valve of *Congeria subglobosa* Partsch is evidence that some fossil dreissenids were adapted to a similar mode of life.

The habit of forming clusters is probably a reflection of the fact that byssally attached epifaunal bivalves, such as many Dreissenacea and Mytilacea, often need to exploit every suitable piece of hard substrate. The pallial line in *Dreissena* (s.l.), *Mytilopsis* and *Congeria* is normally described as being entire, and the siphons of *D. polymorpha* (Pallas) were described as short (Yonge and Campbell 1968; Morton 1969). Such features are indicative of an epifaunal existence. Morton (1970, p. 567, text-fig. 7) described the pallial line of *Mytilopsis sallei* (Recluz 1849) as not being indented by a sinus. Later, on studying living material of the same species, he described it (1981, p. 30) as having a slight pallial sinus, an unusual feature in an epifaunal species (p. 37), and (p. 39) mentioned that its extensible siphons helped it cope with a high sediment load. However, Morton did not state how far the siphons could extend. These interesting observations led him (1981, p. 30) to reconsider his views on *Congeria zsigmondyi* Halavats, from the Pontian of Hungary (1970, p. 565, text-fig. 4), which he had previously described as lacking a pallial sinus and which he had interpreted as being a byssally attached, infaunal species like the quadrate and globose *Congeria subglobosa* Partsch from the Pannonian of the Vienna Basin (1970, p. 565, text-fig. 3). Morton had argued (1970, p. 569) that, in moving water, the size of the latter species would put a great strain on the byssal apparatus. It seems unlikely that *Congeria* was completely infaunal. It has no pallial sinus, so it may be inferred that the siphons were short as in *Dreissena*. It would almost certainly prefer not to be buried sufficiently for the siphons to be permanently covered by sediment, even though Yonge and Campbell (1968) had described the normally epifaunal *D. polymorpha* as being singularly oblivious to the presence of silt because of its ability to expel massive collections of pseudofaeces. The large size of the byssal notch in *C. subglobosa* (pl. 3, fig. 4) and other large species suggests that the byssus may have been extremely well developed and able to cope with bottom currents, which in the muddy clay facies of the Pannonian were probably not strong. It is difficult to imagine that these large, heavy *Congeria* lived in clumps: they were almost certainly solitary and byssally attached to hard objects such as dead shells (text-fig. 2f).

The pallial sinus which Morton (1981) described in *M. sallei* (pl. 1, fig. 19, herein) and in *C. zsigmondyi* is barely noticeable, consisting of a slight truncation of the posterior portion of the pallial line. These pallial lines are not indented, and it is difficult to justify Morton's comparison (1981, pp. 30, 37) between them and the fully sinupalliate *Dreissenomya* (*Sinucongeria*) *aperta* (Deshayes) (pl. 6, figs. 2, 4). By no means all species assigned to *Mytilopsis* possess this weak pallial sinus. Species in which it may be detected include *M. leucophaetus* (Conrad 1831) (pl. 1, fig. 11), the living type species, and *M. basteroti* (Deshayes in Lamarck, 1836) from the Lower Miocene of Aquitaine (pl. 5, fig. 9). It is almost certain that all species of *Mytilopsis*, whether or not this weak pallial sinus is detectable, were basically epifaunal and byssally attached. *Dreissenomya* (s.l.), in which a definite pallial sinus is present, is thought to have been infaunal. Morton (1970, pp. 564, 568, text-fig. 2) suggested that *D. (S.) aperta* was infaunal and byssally attached as it possessed a byssal notch. However, the commissure in this species is so irregular and variable that it is impossible positively to identify a byssal notch as indicated in Morton's figure. Marinescu (1975, p. 90) stated that the gapes in *D. (Sinucongeria)* were either less important than in *Dreissenomya* (s.s.) or absent altogether. He made no mention of the presence of a byssal notch in either subgenus. *Dreissenomya (D.) schroeckingeri* (Fuchs 1870a), on the other hand, possesses pronounced anterior (pedal) and posterior (siphonal) gapes (Marinescu 1975, p. 78, text-fig. 3). Marinescu also (pp. 105–107) discussed the mode of life of these subgenera. Single valves were less common than specimens with both valves together, found nearly perpendicular to the bedding plane, presumably in life position. The indications are that the Pontian *D. (D.) schroeckingeri* lived at depths of up to 30 cms below the sediment surface and that *D. (S.) aperta* at about 5–7 cm (text-fig. 1b, c). He considered that the earlier, Meotian, species of both subgenera were barely covered, as they often occur as isolated valves, and that juveniles, lacking the posterior gape were also surface dwellers. According to Prof. W. Russell-Hunter (*pers. comm. in* Yonge and Campbell, 1968), juveniles of living *Dreissena* use the foot to move about from time to time and produce a weak byssus with only a few threads for temporary attachment. With growth, the foot becomes less important as an organ of locomotion and a much stronger, more permanent byssus is formed. It seems likely that juvenile

fossil dreissenids had similar habits. It is reasonable to suppose that the earlier species of *Dreissenomya* (s.l.) followed this pattern, but the later, more deeply buried species differed in not being byssally attached as adults. They were possibly strong and rapid burrowers, in a manner comparable to members of the Tellinacea.

Other characters

The opisthodetic ligament and soft parts of *D. polymorpha* (Pallas) are described in detail (Yonge and Campbell 1968; Morton 1969). *Mytilopsis sallei* (Recluz 1849), a member of the only other living genus, is similarly dealt with (Escarbassiere and Almeida 1976; Morton 1981). The shell structure of *D. polymorpha* was studied by Taylor, Kennedy and Hall, (1973) who noted its strong resemblance to that found in the Corbiculacea, a predominantly freshwater superfamily, whilst Archambault-Guezou (1982) noted cylindrical perforations which she considered to be tubules in two other living species, which she placed in *Congerina*, but are here assigned to *Mytilopsis* as *M. leucophaetus* (Conrad) and *M. cochleatus* (Kickx in Nyst, 1835).

Planktotrophic larvae are reported in both living genera (Morton 1969, with further references) for *D. polymorpha* (Pallas), and by Escarbassiere and Almeida (1976, p. 167, fig. 14) for *Mytilopsis sallei* (Recluz). As Morton pointed out, the retention of a free-swimming larva is unique among freshwater bivalves. Morton (1969) showed that *D. polymorpha* possessed a very efficient filtering system that enabled it to live in both fast-running and in relatively static freshwaters. *M. sallei* is similar in this respect and, additionally, is extremely tolerant to salinity changes between 0–50‰ (Escarbassiere and Almeida 1976; Morton 1981). This must be an important factor in its ability to be transported across oceans and also in its survival in tropical estuaries and harbours where salinity can vary enormously between wet and dry seasons.

SYSTEMATIC PALAEOLOGY

Repositories. With the exception of figures reproduced from other works, all figures are of specimens in the British Museum (Natural History). Fossils are in the Palaeontology Department (BMPD) and their registration numbers are prefixed by either L or LL. Recent specimens are in the Zoology Department (BMZD), whose registration numbers frequently refer to a whole sample rather than a single specimen.

Subclass HETERODONTA

Order VENEROIDA

Superfamily DREISSENACEA Gray in Turton, 1840

Diagnosis. Normally mytiliform to modioliform; umbones terminal or nearly so; umbonal septum or shelf present, but sometimes vestigial; edentulous; heteromyarian with anterior adductor muscle attached to septum; gills eulamellibranchiate; shell aragonitic, outer layer of simple and crossed lamellae; inner layer of complex crossed lamellae.

Distribution. Lower Eocene to Recent, Europe, Asia Minor and as far east as Kazakhstan (Aral Sea region). Late Oligocene, Central and tropical South America, spreading northwards into southern and Atlantic seaboard areas of United States during the Neogene. Introduced to India, Hong Kong and Japan. Probably introduced to Fiji and West Africa.

Remarks. The characters mentioned in this diagnosis are discussed in the section on morphology and mode of life, whilst the distribution of the family is dealt with under each genus in turn and in the discussion.

Family DREISSENIDAE Gray in Turton, 1840

Diagnosis. As for superfamily.

Subfamily DREISSENINAE, Gray *in* Turton, 1840

Diagnosis. Umbones terminal; pallial sinus absent or weak; byssal gape usually marked.

Remarks. Living Dreisseninae are usually mytiliform, sometimes triangular or quadrate, and have short, separate, siphons. They are epifaunal, byssally attached in clusters. Distinctions between them and the Dreissenomyinae are discussed under the latter.

Distribution. As for superfamily.

Genus DREISSENA van Beneden, 1835a

(text-fig. 2A).

Type species. *Mytilus (sic) polymorphus* Pallas, 1771, by monotypy. Recent, Europe. (pl. 1, figs. 1–6).

Diagnosis. Mytiliform, smooth except for growth lines, with simple septum on which anterior adductor and pedal-byssal retractor muscles are mounted; apophysis lacking; pallial line entire.

Distribution. Late Miocene (Meotian)-Recent, Europe, northern Asia Minor and as far east as the Aral Sea, and the River Euphrates.

Remarks. Numerous fossil species have been recognized particularly in the Paratethys. Many have very restricted distributions both geographically and stratigraphically and the suspicion remains that some are of little more than local significance. Carinate mytiliform *Dreissena* (s.s.) may be easily distinguished from the non-carinate, more modioliform *D. (Pontodreissena)* and *D. (Modiolodreissena)*, but the differences between these do not seem great.

Subgenus DREISSENA van Beneden, 1835a

Plate 1, figs. 1–6.

Diagnosis. *Dreissena* with straight dorsal margin and markedly angular diagonal carina.

Distribution. As for genus (s.l.)

Remarks. *Dreissena* (s.s.) corresponds to the *carinatae*-group of Andrussov (1897–8). The living type species, *D. polymorpha* is long ranging, first occurring in the Meotian of the eastern Paratethys (Iljina *et al.* 1976). Archambault-Guezou (1976b) and Locard (1893) gave useful summaries of its spread from its apparent area of origin. Much of its dispersal through the rivers and canals of western Europe has occurred very recently, being recorded from the Danube in 1769, England in 1824 and the south of France by 1865–6. This rapid spread probably coincided with increasing trade and the interconnections of inland waterways by canals and locks. Locard (1883) described two species from the upper reaches of the Euphrates river system in northern Syria, and later (1893) recorded the genus from above Baghdad. The Holotype (BMZD 1984243) of *Mytilus tenebrosus* Reeve, 1858, described from the Mississippi, is a damaged *D. polymorpha*. It is the only record of the genus from the Western Hemisphere and may be discounted, having either been mislocalized or transported as ballast.

Subgenus PONTODREISSENA Logvinenko and Starabogatov, 1966

Plate 1, figs. 7–10, plate 2, figs. 6–8.

Type species. *Mytilus rostriformis* Deshayes, 1838, by original designation. Pliocene, Crimea, (pl. 1, figs. 7–10, pl. 2, figs. 6–8).

Diagnosis. Dorsal margin convex; ventral margin slightly concave behind umbone; not tumid, diagonal ridge much weaker than in *D. (Dreissena)* and mainly confined to umbonal region; septum broad.

Distribution. Late Miocene (Meotian) to Recent, Paratethys and bordering Mediterranean (see below).

Remarks. The work in which this subgenus was erected has not been seen. *Pontodreissena* is used by Starabogatov (1970), Babak (1983) and Rozanov (1986). *Pontodreissena* corresponds to part of the *modioliformes*-group of Andrussov (1897–8); other members of this group were assigned to *D. (Modiolodreissena)* by Babak (1983). *D. (P.) rostriformis* is first recorded from the Meotian of the eastern Paratethys (Rozanov 1986) though other authors do not recognize it before the Pontian. Archambault-Guezou (1976*b*) summarizes its distribution. In her opinion, it originated in the Dacian Basin during the Lower Pontian and persisted there through the Dacian, invading the eastern Paratethys during the Middle Pontian, continuing there throughout the Pliocene and into the Quaternary, and living now in the Caspian. It invaded the Mediterranean, being found in strata of probable Messinian age from Greece, Italy, Sicily, southern France and southern Spain. Other species are shorter ranging, mainly confined to the eastern Paratethys, and all extinct (Babak 1983).

Subgenus MODIOLODREISSENA Babak, 1983

Plate 2, figs. 3, 4.

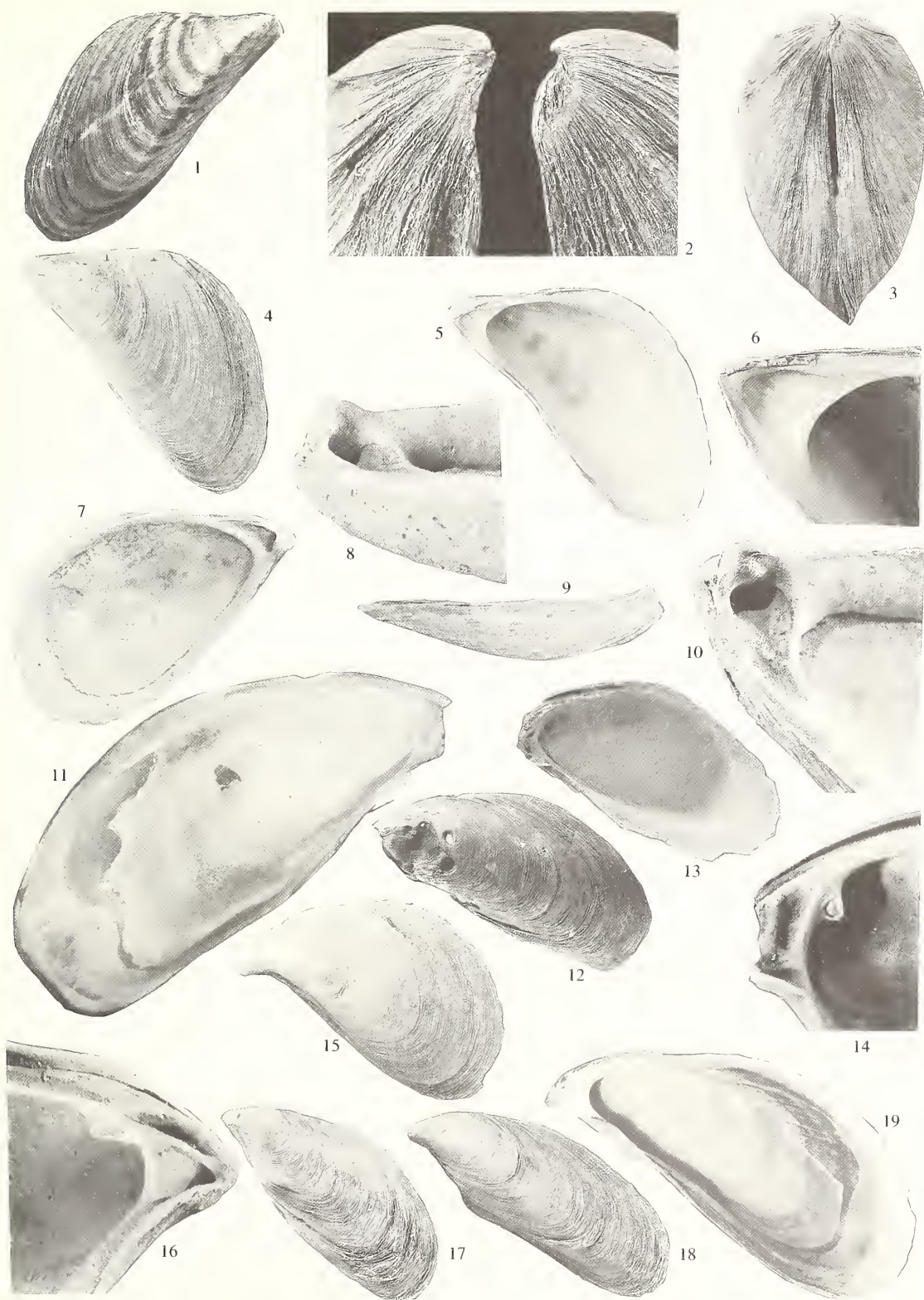
Type species. *Dreissensia theodori* Andrussov, 1893, by original designation, Pliocene, Crimea, (pl. 2, figs. 3, 4).

Diagnosis. Like *D. (Pontodreissena)* but amygdaloidal with both dorsal and ventral margins convexly curved; diagonal ridge lacking.

Distribution. Late Miocene (Meotian) – Late Pliocene (Akchagylia), Paratethys only.

EXPLANATION OF PLATE I

- Figs. 1–6. *Dreissena (D.) polymorpha* (Pallas), sample BMZD 1984242, Recent, Commercial Docks, London, G.B. Sowerby Colln. 1, right valve. 2, 3, ventral views (left valve on right of figures) to show different profiles of commissures in beak region (compare with fig. 8, below), and also byssal notch in fig. 3. 4, left valve. 5, 6, right valve, internal view showing septum. $\times 2$, except 2, 6, both $\times 5$.
- Figs. 7–10. *Dreissena (Pontodreissena) rostriformis* (Deshayes 1838), LL 28238/1 left valve, Pliocene, exact horizon unknown, Kamych-Burun, Kerch Peninsula, Crimea, U.S.S.R. 7, internal, $\times 1.5$. 8, 10, details of septum and rostrate process from different angles, both $\times 4$. 9, ventral view, showing rostrate process (compare with fig. 2 above), $\times 1.5$.
- Figs. 11–14. *Mytilopsis leucophaetus* (Conrad 1831) sample BMZD 1984239, Recent, Green Cove Springs, Black Creek (tributary of St John's River), Florida, attached to submerged wood, collected live by Messrs D. C. Marelli and M. J. Greenberg. 11, 12, left valve internal, showing slight pallial sinus, $\times 5$, external view $\times 3$. 13, right valve internal, $\times 3$. 14, umbonal area of another right valve, tilted to show apophysis, $\times 10$. (N.B. The umbones of this species invariably seem to be eroded).
- Figs. 15, 16, 18, 19. *Mytilopsis salei* (Recluz 1849). 15, sample BMZD 1984230, left valve of shell figured as *Mytilus salei* by Reeve, 1858, pl. 10, fig. 44, Central America, Cuming Colln, $\times 2.5$. 16, left valve of shell from same sample, detail of septum and apophysis, $\times 10$. 18, sample 1984236, left valve of shell figured as *Mytilus domingensis* Recluz (1852) by Reeve, 1858, pl. 100, fig. 44, Dominican Republic, Cuming Colln, $\times 2$. 19, right valve of shell from same sample showing extremely weak pallial sinus, $\times 2.5$.
- Fig. 17. *Mytilopsis africanus* (van Beneden 1835*b*), sample BMZD 1984238, left valve of shell figured as *Mytilus africanus* by Reeve, 1858, pl. 10, fig. 47, Senegal, Cuming Colln, $\times 1.5$, cf. figs. 18 and 19.



NUTTALL, *Dreissena*, *D. (Pontodreissena)* and *Mytilopsis*

Remarks. The broad septum often extends some distance along the dorsal margin. The *modioliformes*-group of Andrussov (1897–8) is split between this subgenus and *D. (Pontodreissena)*: the distinctions between them do not seem great, but may be useful in the context of Paratethys geology. Rozanov (1986) records *D. rinestiensis* (Fontannes 1887) from the Meotian, the species survives to the top of the Pontian in Rumania. The type species first occurs in the late Pontian (Kamyschburun, Kertsch Peninsula) and persists into the Akchagylia.

Genus CONGERIA Partsch, 1835

Plate 2, figs. 1–3, Plate 3, figs. 1–6, text-fig. 2b.

Type species. *Congeria subglobosa* Partsch, 1835, subsequent designation by Pilsbry, 1911, Upper Miocene, Pannonian, Vienna Basin, (pl. 3, figs. 1–6). = *Globocongeria* Taktakishvili, 1973, p. 14, (objective synonym), type species *Congeria subglobosa* Partsch, 1835, by original designation, = *Rhombocongeria* Starabogatov, 1970, type species *Congeria rhomboidea* M. Hörnes, 1870, by original designation, Upper Miocene, Pontian, Hungary, (pl. 2, figs. 1–3) = *Rhomboidea* Marinescu, 1973, (objective synonym of *Rhombocongeria*), type species *Congeria rhomboidea* Hörnes, 1870, by original designation.

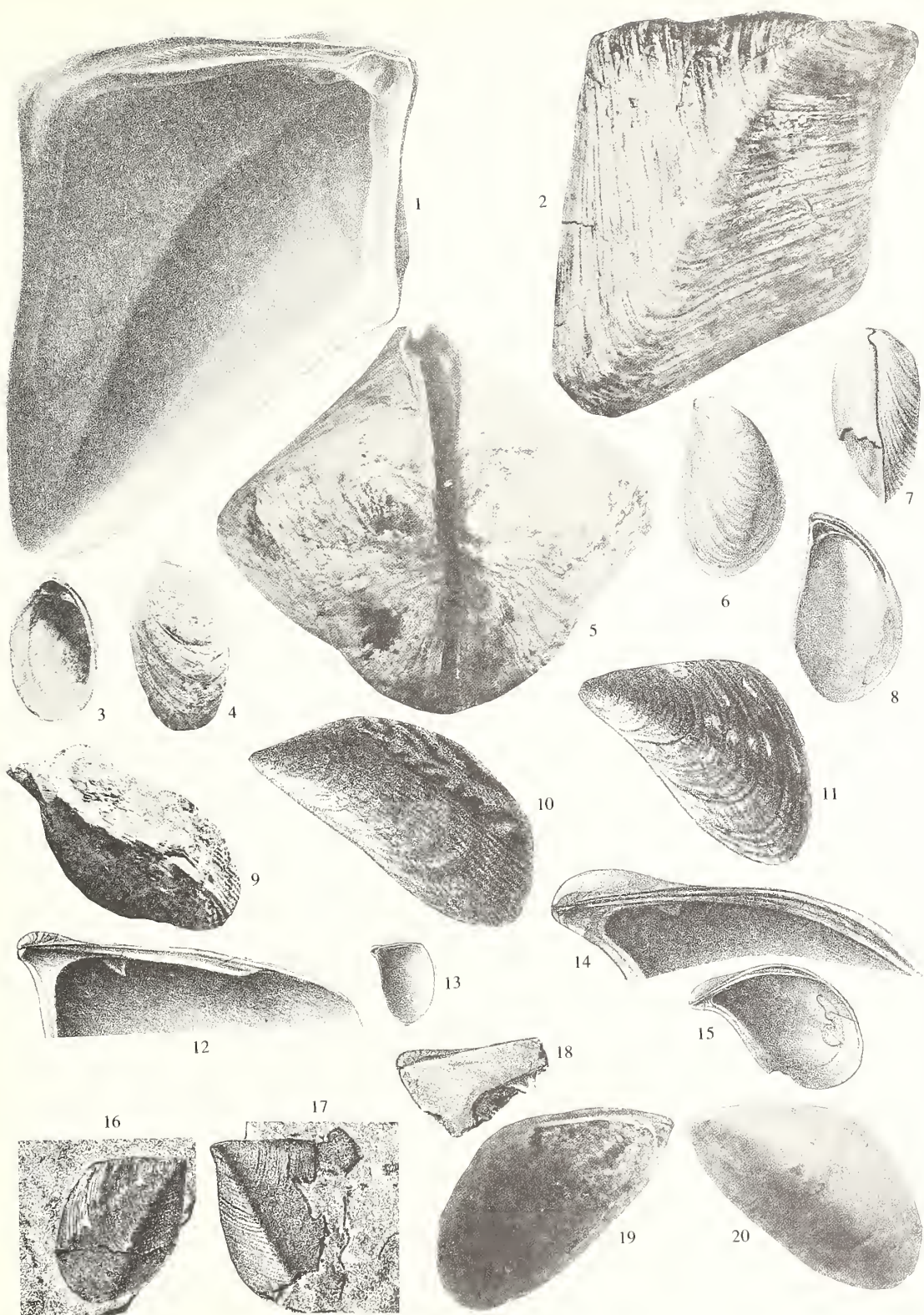
Diagnosis. Quadrate to rhomboidal; smooth except for growth lines; apophysis fused to septum; pallial line entire.

Distribution. Late Miocene (Pannonian to Lower and Middle Pontian), western Paratethys only.

Remarks. There is more than one approach to the classification of dreissenids possessing an apophysis as well as a septum. The first, with variations, adopted by most Eastern Hemisphere authors (Andrussov 1897–8; Orlov 1960; Starabogatov 1970; Taktakishvili 1973; Marinescu 1973;

EXPLANATION OF PLATE 2

- Figs. 1, 2, 5. *Congeria rhomboidea* M. Hörnes, presumed Upper Miocene, Pontian, 1, left valve internal, Árpád, S.E. of Fünfkirchen, southern Hungary, from M. Hörnes, 1867, pl. 48, fig. 4a. 2, 5, right valve and anterior view, from Andrussov, 1897, pl. 10, figs. 8, 10. 2, Ogrugliak, Croatia, Yugoslavia, 5, Árpád, Hungary, all $\times 1$.
- Figs. 3, 4. *Dreissena (Modiolodreissena) theodori* Andrussov (1893), Pliocene, late Kimmerian or early Akchagylia, Eisenerzschichton, Kamych-Burun, Kerch Peninsula, Crimea, U.S.S.R., from Andrussov, 1897, pl. 13, figs. 16, 15. 3, right valve internal. 4, left valve, both $\times 2$.
- Figs. 6–8. *Dreissena (Pontodreissena) rostriformis* (Deshayes 1838), presumed Pliocene, exact horizon and locality unknown, Crimea, U.S.S.R. from Deshayes, 1838, pl. 4, figs. 14–16. 6, left valve. 7, ventral view, with left valve on right of drawing. 8, right valve internal, all $\times 1$.
- Fig. 9. *Prodreissensia perrandoi* Rovereto, Lower Oligocene, TONGRIAN, Mioglia, Liguria, Italy, left valve of the figured syntype, from Rovereto, 1990, pl. 4, fig. 14, $\times 1.5$.
- Figs. 10, 11. *?Prodreissensia euchroma* (Oppenheim 1891), Lower Eocene, Mt. Pulli, near Valdagno, Vicentin, Italy, figured syntypes, from Oppenheim, 1891, pl. 51, figs. 5a, 6a. 10, $\times 4$; 11, $\times 2$.
- Figs. 12, 13. *Mytilopsis chonioides* (Cossmann), Upper Eocene, Priabonian, Le Ruel, Seine-et-Oise, France, right valve of Cossmann's (1887, pl. 6, figs. 32, 33) figured syntype, as refigured by Oppenheim, 1891, pl. 51, figs. 1, 1a, approx. $\times 6$, $\times 1$.
- Figs. 14, 15. *Mytilopsis curvirostris* (Cossmann), Eocene, Priabonian, Marines, Seine-et-Oise, France, right valve of Cossmann's (1887, pl. 6, figs. 29, 30) figured syntype, as refigured by Oppenheim, 1891, pl. 51, figs. 2, 2a, approx. $\times 5$, $\times 1.67$.
- Figs. 16, 17, 18. *Mytilopsis eocenica* (Oppenheim, 1891), Lower Eocene, Dorogh, near Gran, northern Hungary, from Oppenheim, 1891, pl. 51, figs. 8b, d, f, 16 internal view of right valve umbonal region; 17, left valve; 18, right valve, magnifications unknown.
- Figs. 19, 20. *Mytilopsis modiolopsis* (Andrussov, 1897–8), Upper Miocene, Meotian, Akmanajsky, Crimea, U.S.S.R., left valve, internal, external, from Andrussov; 1897, pl. 9, figs. 10, 9, $\times 3$.



Archambault-Guezou 1976a, b, 1982; Babak 1983) is to place them all in a varying number of subgenera or 'groups' of *Congeria* Partsch, the first valid name available. The second view is that adopted by Keen (*in* Moore 1969) who recognized *Mytilopsis* as a separate genus with a basically Western Hemisphere distribution. A modification of these two views, along with, in some cases radical, revision of the stratigraphic and geographic ranges of the subgenera concerned is adopted herein. The basic argument for this decision relies on the fact that mytiliform species resembling living *Mytilopsis* are the first dreissenids to appear in the Eocene, being recorded from all provinces in which dreissenids are found at that time. In contrast, the large, heavy and often quadrate rather than mytiliform species, typified by *C. subglobosa*, occur only at about the Miocene-Pliocene boundary in the western Paratethys. *Congeria* is here regarded as a short-lived offshoot of *Mytilopsis*.

Andrussov's (1897-8) divisions of *Congeria* into various non-binomial 'groups', for some of which he designated 'type-species' have been validated subsequently, and some have junior synonyms (see Table 2).

Comparatively few species remain in *Congeria*. Most are illustrated and listed as members of the *subglobosae* and *rhomboidea* groups by Andrussov (1897-8). They are recorded from the Vienna Basin, Yugoslavia, Hungary and Rumania. *C. subglobosa* Partsch was first described from the Plattensee (Lake Balaton) district of Hungary and is common in the Pannonian of the Vienna Basin. *C. rhomboidea* M. Hörnes, was first described from Hungary and, in common with other species assigned to *C. (Rhomboides)* by Marinescu (1973), is confined to the Lower and Middle Pontian (Odessian and Portaferrian).

Some confusion may exist about the status of *Globocongeria*. Taktakishvili (1973, p. 14) designated *C. subglobosa* Partsch as type species, thus making it an objective synonym of *Congeria* (s.s.) itself. Taktakishvili's interpretation of *Congeria* (s.s.) was that it corresponded to the *mytiliformes* and *eocenes* groups of Andrussov, both of which are here placed in *Mytilopsis*. Unfortunately the *Zoological Record (Mollusca)* for 1978, p. 425 quoted the type species of *Globocongeria* as being *Congeria digitifera* Andrussov, 1897-8. This, in fact, was merely the first species dealt with by Taktakishvili (1973, p. 36) in his formal descriptions of the Pliocene dreissenids of western Georgia. All the species assigned by Taktakishvili to *Globocongeria* belong to Andrussov's *subglobosae* group, and thus to *Congeria* (s.s.).

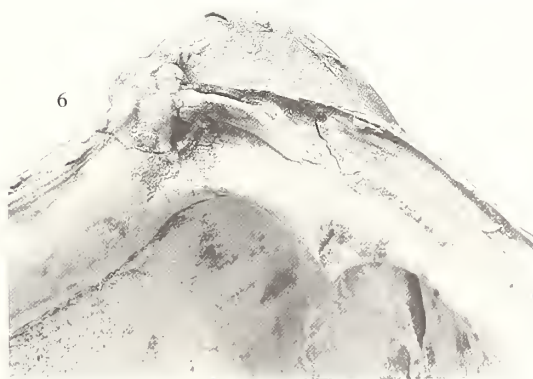
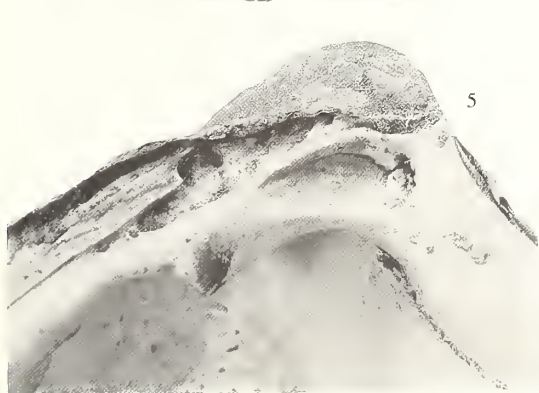
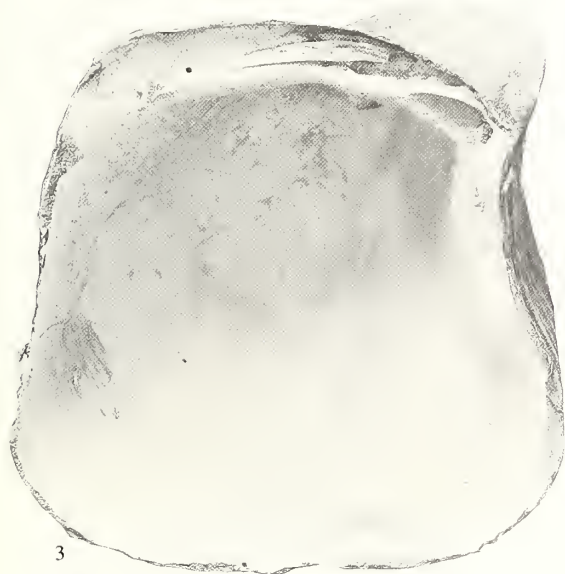
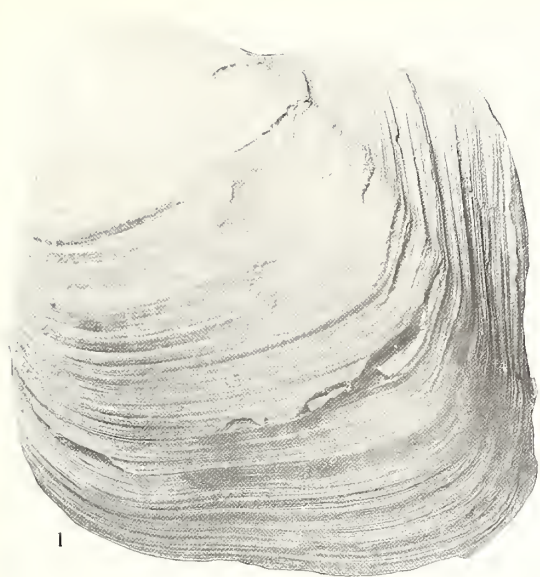
Genus MYTILOPSIS Conrad, 1858

Plate 1, figs. 11-19; Plate 2, figs. 12-20; Plate 4, figs. 1-16; Plate 5, figs. 6-13; Plate 6, figs. 8-10; text-figs. 2A, E.

Type species. *Mytilus leucophaetus* Conrad, 1831, subsequent designation by Dall, 1898, Recent, eastern U.S.A., (pl. 1, figs. 11-14). = *Andrusoviconcha* Starabogatov, 1970, type species *Congeria modiolopsis* Andrussov, 1897-8, by original designation, Upper Miocene, Meotian, Crimea, (pl. 2, figs. 19, 20). = *Eocongeria* Starabogatov, 1970, type species *Tichogonia (Congeria) eocenica* Oppenheim, 1891 (see remarks), by original designation, Lower Eocene, Hungary, (pl. 2, figs. 16-18). = *Mytilia* Marinescu, 1973, type species *Congeria neumayri* Andrussov, 1897-8, by original designation (preoccupied by *Mytilia* Gray, 1858, Reptilia and by *Mytilia* Gosse *in* Hudson and Gosse, 1886, Rotifera), = *Modiola* Marinescu, 1973, type species *Congeria cizeki* Hörnes, 1867, by original designation (preoccupied by *Modiola* Lamarck, 1801, Mollusca), =

EXPLANATION OF PLATE 3

Figs. 1-6. *Congeria subglobosa* Partsch, Upper Miocene, Pannonian, Austria. 1, 2, 3, 5, 6. LL 28239., Brunn, near Vienna, (ex K.K. Mineralien-Kabinet), 1, left valve, $\times 1$. 2, right valve, internal, $\times 1$. 3, left valve internal, $\times 1$. 5, left valve, tilted, to show apophysis, $\times 1.5$. 6, right valve, tilted to show apophysis, $\times 1.5$. 4, LL 28240/1. Hennesdorf Brick Pit, 10 km S. of Vienna, F. Rögl, B. R. Rosen and J. G. Darrell Colln, front view showing byssal notch, $\times 1$.



Trigouipraxis Starobogatov, 1970, type species *Congerina triangularis* Partsch, 1835, by original designation, Upper Miocene, Pannonian, Hungary, (pl. 4, figs. 1–5). = *Triangularia* Marinescu, 1973, type species *Congerina ornithopsis* Brusina, 1892, by original designation, (preoccupied by *Triangularia* Frech, 1894, Mollusca).

Diagnosis. Like *Dreissena*, but possessing an apophysis, usually behind, but sometimes partly underneath and partially fused to the septum; pallial sinus, if present, very weak.

Distribution. Lower Eocene – Pliocene, Europe; late Oligocene – Recent, central and northern South America and Caribbean, spreading to North America bordering Gulf of Mexico and Atlantic. Introduced (Recent), southern India, Japan and Hong Kong, probably introduced, Fiji, West Africa and Rhine – Scheldt Delta.

Remarks. The generic synonymy and its relationship to Andrussov's (1897–8) 'groups' is best explained by reference to Table 2, whilst the main reasons for placing these taxa in *Mytilopsis* rather than *Congerina* are given in the remarks on the latter genus. Andrussov (1897–8) placed all the living Western Hemisphere nominal species of *Mytilopsis*, including the type species *M. leucophaetus* and *M. sallei* (Recluz 1849) (pl. 1, figs. 15, 16, 18, 19), into his 'mytiliformes'-group, whilst he placed the living European *M. cochleata* (Kickx in Nyst, 1835) and the West African *M. africanus* (van Beneden 1835b) (pl. 1, fig. 17) into his 'modioliformes'.

It would appear, however, (Nuttall 1990, pp. 282, 284, fig. 335) that *M. africanus* is synonymous with the form of *M. sallei* originally described as *M. domingensis* (Recluz 1852) (pl. 1, fig. 19) from the Dominican Republic. It is suggested (S. Morris, BMZD, *pers. comm.*) that this African occurrence may well be the result of introduction by man, perhaps during the period of the slave trade between West Africa and the West Indies. *M. cochleata* is also likely to have been introduced to the Rhine-Scheldt Delta from the Western Hemisphere. Variation within species is such that there is no apparent reason for the separation of Recent 'mytiliformes' from 'modioliformes'.

Starobogatov (1970, p. 83) designated, as type species of *Eocongerina*, a new subgenus of *Congerina*, *Dreysensia* (*Congerina*) *eocenica* Munier-Chalmas in Hébert and Munier-Chalmas (1877, p. 126), even though the name appears only in a faunal list and is clearly a *nomen nudum*. Oppenheim (1891, p. 953) was the first to describe the species and is here credited with its authorship. Members of the 'eocenae'-group of Andrussov, upon which *Eocongerina* is based, are all of Eocene age and exhibit a wide variation in shell shape, but most are typical of *Mytilopsis*. *D. eocenica* from the Lower Eocene (Eames in Morley Davies, 1975, p. 146) of Dorogh, Hungary, possesses a low angular fold not normally seen in *Mytilopsis*, but the form of its septum and apophysis is indistinguishable from that of modern *Mytilopsis*. Oppenheim (1891, pl. 51) gave excellent illustrations, including the internal characters, of this and three other Eocene species, *C. chonioides* (pl. 2, figs. 12, 13) and *C. curvirostris* (pl. 2, figs. 14, 15) both described by Cossmann (1887) from the French upper Eocene.

EXPLANATION OF PLATE 4

Figs. 1–5. *Mytilopsis triangularis* (Partsch), Upper Miocene, Pontian, Radmanest, Banat, Hungary. 1, 4, 5, L19499/1, left valve, 1, interior, tilted, showing typical *Mytilopsis* apophysis, $\times 4$. A, 4 interior, $\times 1.5$. 5, exterior, $\times 1.5$. 2, 3, L19499/2, right valve. 2, interior, $\times 1.5$. 3, interior, tilted, $\times 4$.

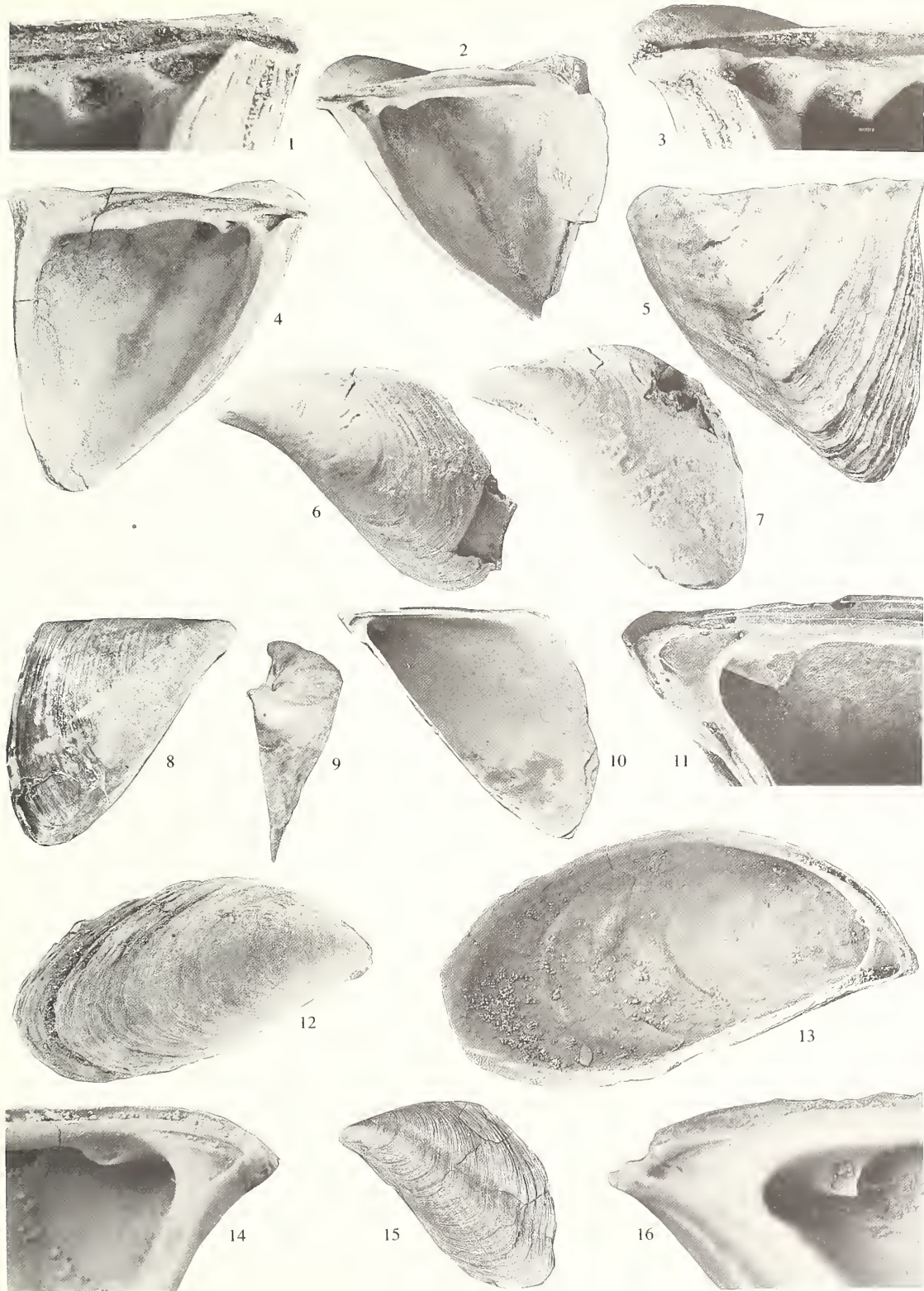
Figs. 6–11. All from Miocene, Pebasian, Peru.

Fig. 6. *Mytilopsis sallei* Recluz (1849), LL 27195, left valve, Panamá, $\times 3$.

Fig. 7. *Mytilopsis scripta* (Conrad 1874), LL 27956, left valve, Pichana, $\times 2.5$.

Figs. 8–11. *Mytilopsis* cf. *scripta* (Conrad 1874), LL 27914, right valve, Panamá. 8, external; 9, anterior; 10, internal, all $\times 5$. 11, internal, showing apophysis, $\times 20$.

Figs. 12–16. *Mytilopsis sowerbyi* d'Orbigny (1850), Upper Eocene, Priabonian, Lower Headon Beds, all Hordwell (except 15, Mead End) Hampshire. 12, LL 28131, Edwards Colln, right valve, $\times 4$. 13, LL 28130, left valve internal $\times 4$. 14, 16, LL 28242/1, 2, Hastings Colln, internal views of umbonal region, tilted to show apophysis lying under septum. 14, left valve; 16, right valve, both $\times 10$. 15, LL 28244, Edwards Colln, left valve, $\times 2$.



and of *C. euchroma* Oppenheim, 1891, (pl. 2, figs. 10, 11) from the northern Italian Eocene. Andrussov (1897) recorded *C. curvirostris* as the basal member of his 'mytiliformes'-group (= *Mytilia*) and *C. euchroma* along with the British Priabonian *D. sowerbyi* (d'Orbigny 1850) (pl. 4, figs. 12–16) as one of the earliest 'modioliformes'. In the present work *C. euchroma* is provisionally placed in *Prodreissensia* because it possesses radiating ribbing whilst the other species mentioned above are considered to be typical of *Mytilopsis*. Thus, there seems as little reason for either generic or subgeneric separation of these early members of the family, as there is for separating the living species discussed in the preceeding paragraph.

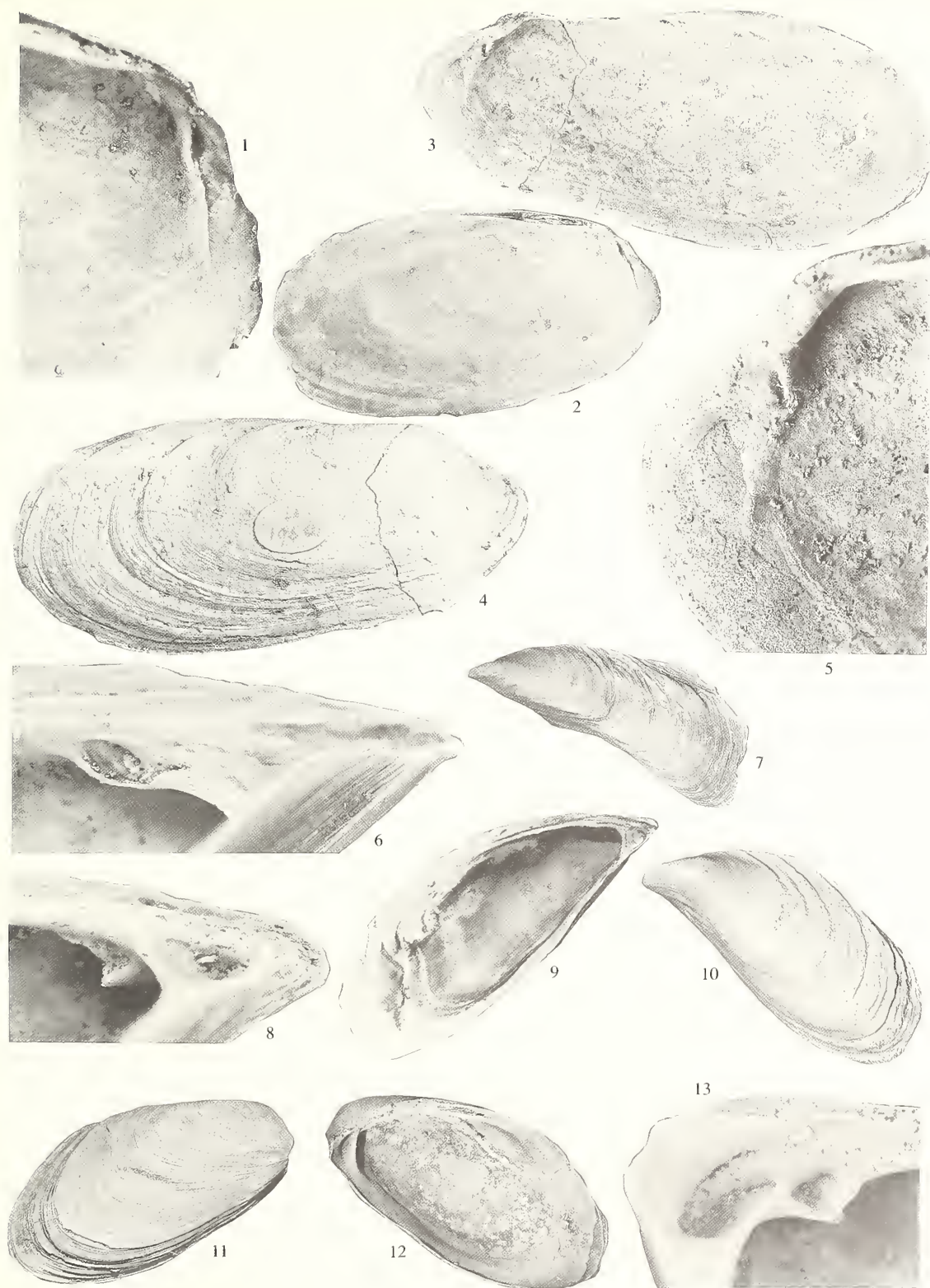
During the Eocene *Mytilopsis* is represented by several species (Oppenheim 1891; Andrussov 1897–8) including *M. eocenica* (Oppenheim 1891), Lower Eocene, Dorogh, Hungary; *M. curvirostris* and *M. chonioides* (both Cossmann 1887) rare in the Sables Moyens (Bartonian = Priabonian) of the Paris Basin (Cossmann and Pissarro 1904–6) and *M. sowerbyi* (d'Orbigny 1850) from the Lower Headon Beds (Priabonian), of Hampshire and the Isle of Wight, England (BMPD).

Oligocene species include *M. nystiana* (d'Orbigny 1852), Tongrian (= Lattorfian), Belgium (Glibert and de Heinzelin 1954 as *Congerina nysti*) and *M. aralensis* (Merklin 1974), Middle Oligocene, Aral Sea Region, USSR. *M. brardi* (Brongniart 1823) was recorded (Wenz 1921) from the Cerithien-schichten of the Mainz Basin, now dated as Chattian (Martini in Steininger *et al.* 1985, p. 334). This species persists into the Miocene, occurring in the Aquitanian *Corbicula*-Schichten and overlaying Hydrobien-Schichten (Wenz 1921). Widespread Miocene occurrences include *M. amygdaloides* (Dunker 1848), (pl. 5, figs. 11–13) probably late Lower Miocene, Wurttemberg, Germany (BMPD); *M. alta* (Sandberger 1874), Middle Miocene (Pontilévian), Faluns of Touraine, France (Glibert and van de Poel 1967); several species from the Aquitanian to Helvetian of the Aquitaine Basin, France, including (pl. 5, figs. 8–10) *M. basteroti* (Deshayes in Lamarck, 1836) (see Cossmann and Peyrot 1914; BMPD); *M. sandbergeri* (Andrussov 1897–8), Miocene, Poland (Friedberg 1936); *M. sandbergeri*, Miocene (Konkian and Tortonian), and several species up to the Meotian, of the Ukraine (Zelinskaya *et al.* 1968); *M. soceni* and *M. moesia* (both Jekelius, 1944) Sarmatian, Rumania and also Vienna Basin (Papp 1954; Sieber 1955); *M. spatulata* (Parsch 1835) (pl. 5, figs. 6, 7, text-fig. 2E) and several other species, Pannonian, Vienna Basin (Papp 1951, 1953; Sieber 1955); several species, Meotian, Paratethys (Rozanov 1986); *M. subcarinatus* (Deshayes 1838), Pontian and Lower Kimmerian, Paratethys, and other species of which the last surviving were *M. mirabilis* (Seninsky 1905) and *M. caucasica* (Seninsky 1905) (see Babak 1983, p. 87), both of which died out in the late Kimmerian.

In Western Europe, the last surviving, naturally occurring *Mytilopsis* appears to be *M. rhodanica* (Fontannes 1882) from the 'Infra-Pliocene' (Messinian) of the Rhone Valley. According to Archambault-Guezou (1976b) this species was derived from *M. subcarinatus* (Deshayes 1838) of the Paratethys, having migrated into the Mediterranean in the same way as *Dreissena* (*Pontodreissena*) *rostriformis* (Deshayes 1838) (see above).

EXPLANATION OF PLATE 5

- Figs. 1–5. *Dreissenomya* (*D.*) *schroeckingeri*, (Fuchs, 1870a), Upper Miocene, Pontian, Radmanest, Banate, Hungary. 1, 2, L71745, left valve interior, 1, $\times 4$; 2, $\times 1.5$. 3–5, L19501, right valve, 3, 4, $\times 1.5$; 5, $\times 4$.
 Figs. 6, 7. *Mytilopsis spatulata* (Parsch), L23908/1, left valve, Upper Miocene, Pannonian, Brunn, near Vienna, Austria. 6, detail of internal umbonal region, tilted, apophysis attached to posterior of septum (right valve has similar arrangement), $\times 10$. 7, $\times 2$.
 Figs. 8–10. *Mytilopsis basteroti* (Deshayes 1836), Lower Miocene, Aquitanian or Burdigalian, Dax, Landes, France, Deshayes Colln. 8, 9, LL 28240/1, left valve, 8, internal view of worn umbonal region, $\times 10$. 9, to show weak pallial sinus, $\times 2.5$. 10, LL 28240/2, left valve, $\times 2$.
 Figs. 11–13. *Mytilopsis amygdaloides* (Dunker, 1848), probably late Lower Miocene, Unterkirchberg, Bavaria, L1266/1, left valve, 11, 12, $\times 2.5$. 13, tilted to show apophysis, $\times 10$.



The Western Hemisphere distribution of *Mytilopsis*, the only dreissenid to reach the New World, is discussed in detail by Nuttall (1990, pp. 278–280, figs. 319–325). The first occurrences, some thirty million years later than the appearance of the genus in Europe, are of *M. trigalensis* (Olsson 1931) from the late Oligocene of the Pacific coastal region of Peru and of *M. dalli* (Clerc in Joukowsky, 1906) from rocks of similar age in Western Panama. *M. trigalensis* may well be conspecific with the later (Miocene, but now extinct) *M. scripta* (Conrad 1874) (pl. 4, fig. 7) from the Pebas Beds of the Upper Amazon Valley. Until the appearance of the Panama landbridge in the Pliocene, South America was an island with the result that the Caribbean and tropical eastern Pacific areas formed one faunal province. The presence of the living Caribbean *M. sallei* (Recluz 1849) (pl. 4, fig. 6) in the Pebas Beds and other Miocene occurrences of *M. scripta* in the Magdalena Valley and at La Tagua in the Oriente of Colombia suggest that *Mytilopsis* invaded the Upper Amazon Valley from the Caribbean. *M. dalli* is very similar to *M. sallei* and may be synonymous. *M. sallei* also occurs in the Miocene of the Dominican Republic. The living type species of *Mytilopsis*, *M. leucophaetus* (Conrad) is not known before the Pliocene. It is recorded as *M. jamaicensis* (Woodring 1925) from the Bowden Beds (now known to be Pliocene) of Jamaica. A series of shells (LL28109–29) from the Plio-Pleistocene Caloosahatchee Formation of Florida originally identified as *Congeria lamellata* Dall (1898) appears to be a mixture of *M. sallei* and *M. leucophaetus*. Detailed distribution maps of the two species at the present day are given by Marelli and Gray (1983). They show that they overlap in this region nowadays and that *M. leucophaetus* now occurs as far north as the Hudson River. The apparent lack of fossil records from the eastern seaboard of the United States points to this northward extension of its distribution being the result of introduction.

A distribution map given by Starabogatov (1970, fig. 12) erroneously shows *Mytilopsis* as occurring over much of north-eastern South America including the Amazon Basin and the northern Brazilian coastal strip as far south-east as Recife (Pernambuco). Dunker (1853), who described *Tichogonia rosmaessleri* (a junior synonym of *M. sallei*) from Pernambuco, was himself very dubious about the locality information, and this record can safely be discounted. Although *M. sallei* is widespread on Caribbean islands (Marelli and Gray 1983), it is not encountered further eastward and its presence is not mentioned in the very thorough review of the Surinam fauna (Altena 1971).

On the Pacific coast, *Mytilopsis* is known only from northern South America (Olsson 1961; Keen 1971) at the present day. It is probable that Fijian occurrences (Dall 1898; Hertlein and Hanna 1949) are the result of introduction, though clearly not primarily as a result of the opening of the Panama canal (in 1914) as suggested by Morton (1981). Morton's suggestion that *M. sallei* has been more recently introduced to southern India is supported. The species has subsequently been reported in Victoria Harbour, Hong Kong (Huang and Morton 1983) and in Shimizu Harbour, Honshu, Japan (T. Habe, *pers. comm.* in Huang and Morton), and in Tokyo Bay (Furuse and Hasegawa 1984). There is the possibility, however, that more than one species of *Mytilopsis* has been introduced westwards across the Pacific from the Americas. Marelli and Gray (1985) placed the Fijian *M. alleyniana* Hertlein and Hanna (1949) in the synonymy of *M. adamsi* Morrison (1946), originally described from the Pearl Islands, Panama.

The occurrences of *M. cochleatus* (Kickx in Nyst, 1835) in the Rhine-Scheldt Delta (Adam 1960; Wolff 1969) and of several nominal West African species (Pilsbry and Bequaert 1927, Congo; Binder 1958, 1968, Ivory Coast; Reeve 1857–8, Senegal) are also thought to be the result of introduction.

Records of *Mytilopsis* from the East Indies (Keen in Moore, 1969) and Indonesia (Eames in Morley Davies, 1971) are probably based on the septate *Sinomytilus* Thiele (1934, p. 801), described as a section of *Mytilus* whose type species is *Dreissena crosseana* L. Morlet (1884). Specimens (BMZD 1906.9.19.76–77) of this species and of *D. massiei* L. Morlet (1892) (BMZD 1902.3.22.55), both from Cambodia, confirm Thiele's assignment to the Mytilidae. Their inner shell layer appears to be nacreous.

Trigonopraxis, (pl. 4, figs. 1–5) (the 'triangulares' group of Andrussov 1897–8) is well covered in other literature (Brusina 1892; Jekelius 1944; Papp 1953; Sieber 1955; Marinescu 1973). It is confined to the Pannonian and Pontian of the Pannonian and Dacic Basins. Differences between

nominal species assigned by these authors to this group are mostly slight and there seems to be no compelling reason for subgeneric separation from *Mytilopsis*. This view is supported by the occurrence of rather similar trigonal-shaped *Mytilopsis* (pl. 4, figs. 8–11) in Miocene brackish-water deposits in South America (Nuttall 1990, pp. 285–6, figs. 347, 348).

Genus PRODREISSENSIA Rovereto, 1898

Plate 2, fig. 9.

Types species. *Dreissensia (Prodreissensia) perrandoi* Rovereto, 1898, by original designation, Lower Oligocene, Tongrian, northern Italy, (pl. 2, fig. 9).

Diagnosis. Resembling *Dreissena* but with sculpture of radiating costules; septum present, shell interior otherwise unknown.

Distribution. ?Lower Eocene and Lower Oligocene (Tongrian), northern Italy only.

Remarks. Rovereto (1898, pp. 159, 174) described his single, poorly preserved species from the Tongrian of Mioglia (Liguria) as the type of a new 'section' of *Dreissena* characterized by longitudinal ribbing. The only known illustration is Rovereto's later (1900, pl. 4, fig. 14) external view of his type specimen. Both this and the original description were copied by Sacco (1904, p. 152, pl. 29, fig. 12) who was unable to add any new information about this taxon. The illustration clearly shows both the faint traces of radiating ribs and a strong carinate diagonal ridge. The original specific description mentioned the presence of an area (septum), but gave no other details of the interior. Rovereto (1898, p. 159), presumably because of its strong carination, had compared his species with the much younger *Dreissena guezdai* Brusina, 1884, which was described from near Zagreb and placed by Andrussov (1897–8) in his *Congerina* 'triangulares' group. All other members of Rovereto's rich bivalve fauna are undoubtedly marine, raising the suspicion that this species might be a septate member of the Mytilacea.

Tichogonia (Congeria) euchroma Oppenheim (1891) (pl. 2, figs. 10, 11) from the Lower Eocene, Lignite Marls of Mount Pulli (Vicentin, North Italy) seems to be the only definite species of the Dreissenidae with similar radiating ribbing. Oppenheim's description mentioned the presence of a septum but stated that the Schloss (hinge) and apophysis were as yet unknown. Andrussov (1900, pl. 3, figs. 23, 24) provided photographic illustrations of the exterior of two of Oppenheim's original specimens. The ribs are faint and the diagonal ridge is low and definitely not carinate. The outline is mytiliform as in typical *Mytilopsis* and *Dreissena*. It is possible that *T. (C.) euchroma* and *P. perrandoi* may be related in spite of the differences in shape.

The systematic position of *Prodreissensia perrandoi* cannot be properly assessed because of lack of knowledge of internal details of its shell. Its Palaeogene age, however, would suggest that it is more likely to be an offshoot of *Mytilopsis* rather than *Dreissena*, if it is, in fact, a member of the family. *T. (C.) euchroma*, on the other hand, is definitely a dreissenid.

Subfamily DREISENOMYINAE Babak, 1983

Diagnosis. Shell modioliform, compressed; umbones not terminal; apophysis lacking; sinupalliate; posterior siphonal gape present.

Distribution. Late Miocene-early Pliocene (Meotian-late Pannonian) to top Pliocene (Rumanian), Paratethys only.

Remarks. In comparison with nearly all Dreisseninae the shell is modioliform rather than mytiliform and is laterally compressed. Exceptions include species such as *Mytilopsis amygdaloides* (Dunker) (pl. 5, figs. 11–13), which is slightly modioliform but not compressed, whilst *Dreissena*

(*Pontodreissena*) (pl. 1, figs. 7–10) and *D. (Modiolodreissena)* (pl. 2, figs. 3, 4), though fairly compressed, are basically mytiliform with terminal umbones. In Dreissenomyinae a byssal notch is lacking and an antero-ventral pedal gape may sometimes be observed. The commissure, however, is so irregular that these features, interpreted as adaptations to an infaunal mode of life, are not always readily apparent in most specimens, particularly separated valves. They are therefore omitted from the subfamilial diagnosis.

Babak (1983, p. 60) referred to Dreissenomyinae Taktakishvili, 1973. I have been unable to find any reference to this new subfamilial name either in Taktakishvili's work, or in the 1978 *Zoological Record* which covers his paper. Authorship is therefore tentatively ascribed to Babak (1983).

Genus DREISSENOMYA Fuchs, 1870b

Types species. *Congeria schroeckingeri* Fuchs, 1870a, by original designation. Upper Miocene, Pontian, Hungary, (pl. 5, figs. 1–5, text-figs. 2B, C; 3A, B, D, E).

Diagnosis. As for subfamily.

Distribution. As for subfamily.

Subgenus DREISSENOMYA Fuchs, 1870b

Plate 5, figs. 1–5, text-figs. 2C, 3A, B, D, E.

Diagnosis. Umbones well back from anterior of shell; thin-shelled; both antero-ventral and posterior gapes marked; septum reduced to strong ridge, with anterior adductor and pedal/byssal scars lying partly on and partly anterior to ridge; pallial sinus deep.

Distribution. Late Miocene – early Pliocene (Meotian – late Pannonian) to late Pontian, Paratethys.

Remarks. See under *D. (Sinucongeria)*.

Subgenus SINUCONGERIA Lorenthey, 1894

Plate 6, figs. 1–7, text-fig. 2B, 3C, F.

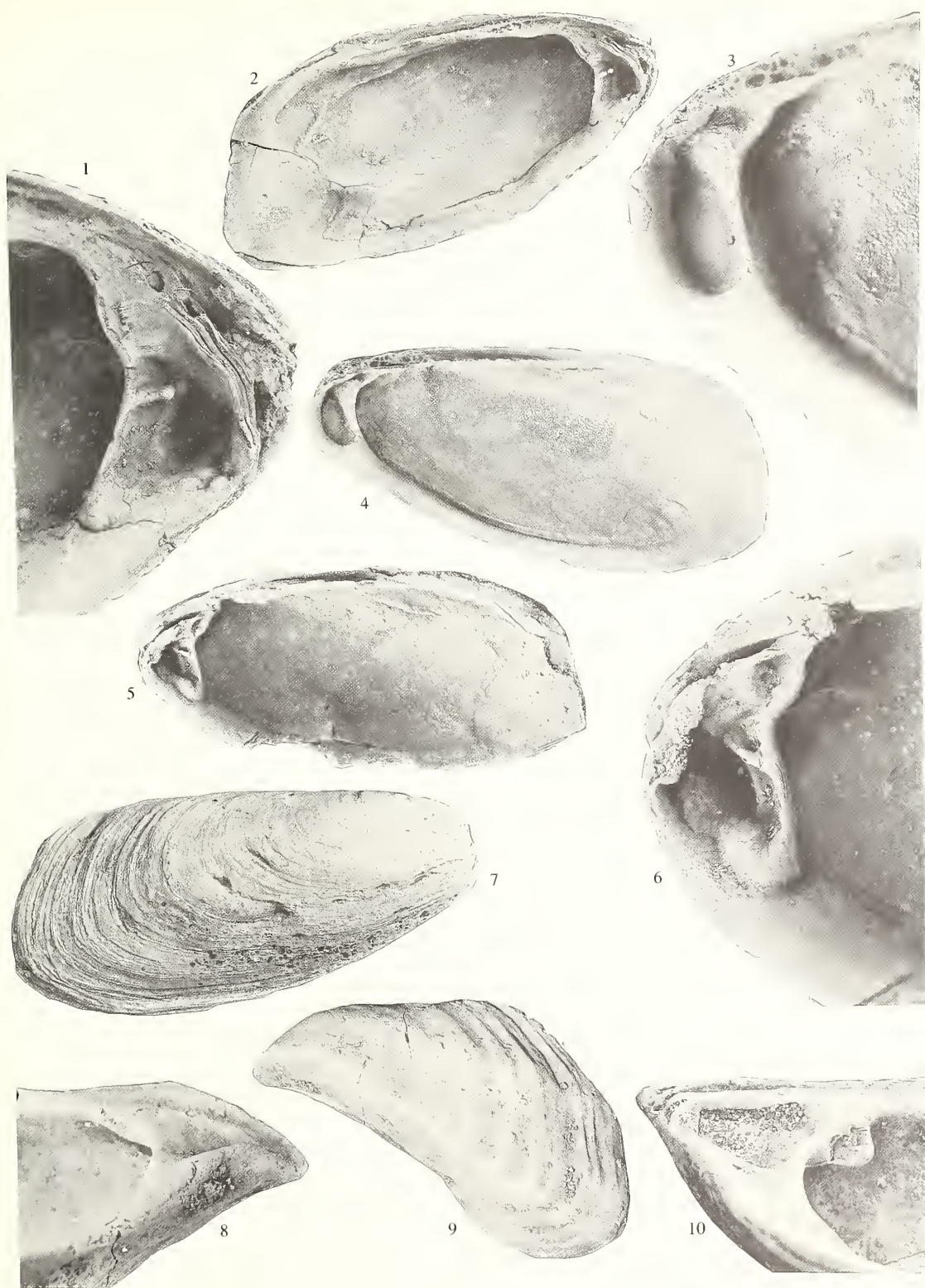
Type species. *Congeria arcuata* Fuchs, 1870a, by monotypy, Upper Miocene, Pontian, Hungary, (text-fig 3C, F).

Diagnosis. Similar to *Dreissenomya* s.s. but thicker shelled; umbones almost terminal; valves more tumid; true septum present, usually bearing irregular ridges; pallial sinus not very deep.

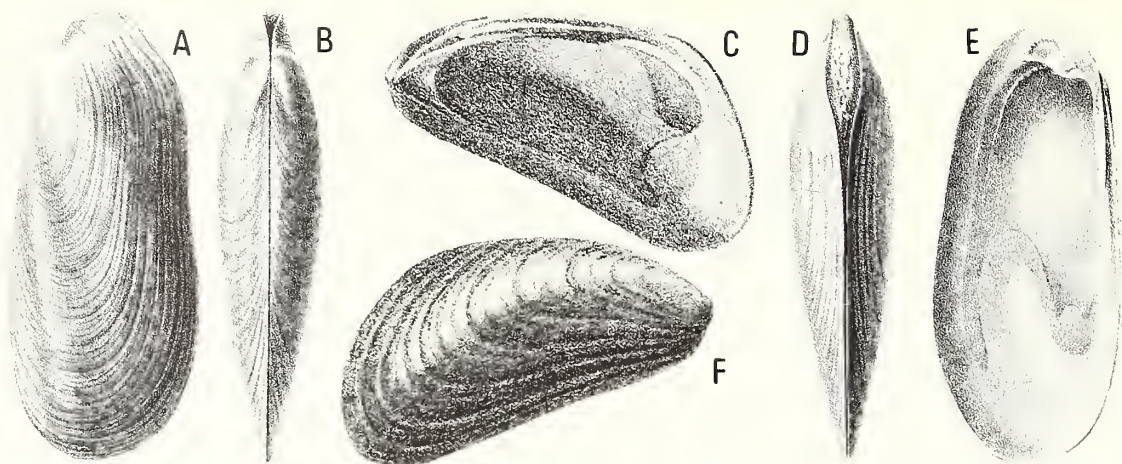
EXPLANATION OF PLATE 6

Figs. 1–7. *Dreissenomya (Sinucongeria) aperta* (Deshayes 1838). 1, 2, 5, 6, LL 18451, Upper Miocene, Upper Pontian (Bosphorian), Stoichitza Valley, Cocorova-Mehedintzi, Rumania, F. Marinescu Colln, (left valve figured Morton 1970, text-fig. 2). 1, 2, left valve interior, $\times 4$, $\times 1.5$. 5, 6, right valve interior, $\times 4$, $\times 1.5$. 3, 4, 7, L19502, probably Pliocene (Kimmerian or Akchagylia), Crimea, U.S.S.R., right valve. 3, 4, interior $\times 4$, $\times 1.5$. 7, exterior, $\times 1.5$.

Figs. 8–10. *Mytilopsis subcarinata botenica* Andrussov (1897–8), ?Top Miocene-basal Pliocene, Upper Pontian, Basinal Govorei, Rumania, ex Muzel Istoria Naturala "Gr. Antipa", Bucharest, 8, 9, LL 9023, 8, left valve internal, tilted, with anterior pedal/byssal attachment fused to posterior wall of septum as in *Congeria*, $\times 3$. 9, same external, $\times 1.5$. 10, LL 9022, right valve internal, tilted, with 'normal' *Mytilopsis* apophysis, $\times 3$.



NUTTALL, *Dreissenomya (Sinucongeria)* and *Mytilopsis*



TEXT-FIG. 3. All from Upper Miocene, Pontian, Radmanest, Banate, Hungary. A, B, D, E. *Dreissenomya* (*D.*) *schroeckingeri* (Fuchs), from Fuchs, 1870*b*, pl. 16, figs. 5–8, $\times 1$. C, F. *Dreissenomya* (*Sinucongeria*) *arcuata* (Fuchs), from Fuchs, 1870*a*, pl. 16, figs. 12, 13, $\times 2$.

Distribution. Late Miocene (Meotian – late Pannonian) to top Pliocene (Rumanian), Paratethys.

Remarks. *Dreissenomya* (s.s.) barely penetrates into the Euxinic Basin, the eastern limit of its distribution being the western Black Sea Coast. *Sinucongeria*, however, is represented there by the long-lived (Pontian-Rumanian), and comparatively widely distributed, *D. (S.) aperta* (Deshayes 1838) (pl. 6, figs. 1–7) which occurs in the Crimea, Kerch Peninsula and as far east as western Georgia, as well as in the Dacian and Pannonian Basins. Marinescu (1975) assigned eight species to *Dreissenomya* (s.s.) and seven to *Sinucongeria*. Although *Dreissenomya* (s.s.) with its markedly non-terminal umbo, greatly reduced septum and deeper pallial sinus, would appear to be further removed from the standard dreissenid pattern than *Sinucongeria*, both subgenera first appear in the Meotian. Marinescu postulated descent from *Congerina* (*Andrussoviconcha*) *novorossica* Sinsow (1877). Archambault-Guezou (1976*a*, pls. 4, 5) provided numerous illustrations of *D. (S.) aperta* (Deshayes) including syntypes, and of *D. (D.) shroeckingeri*.

DISCUSSION

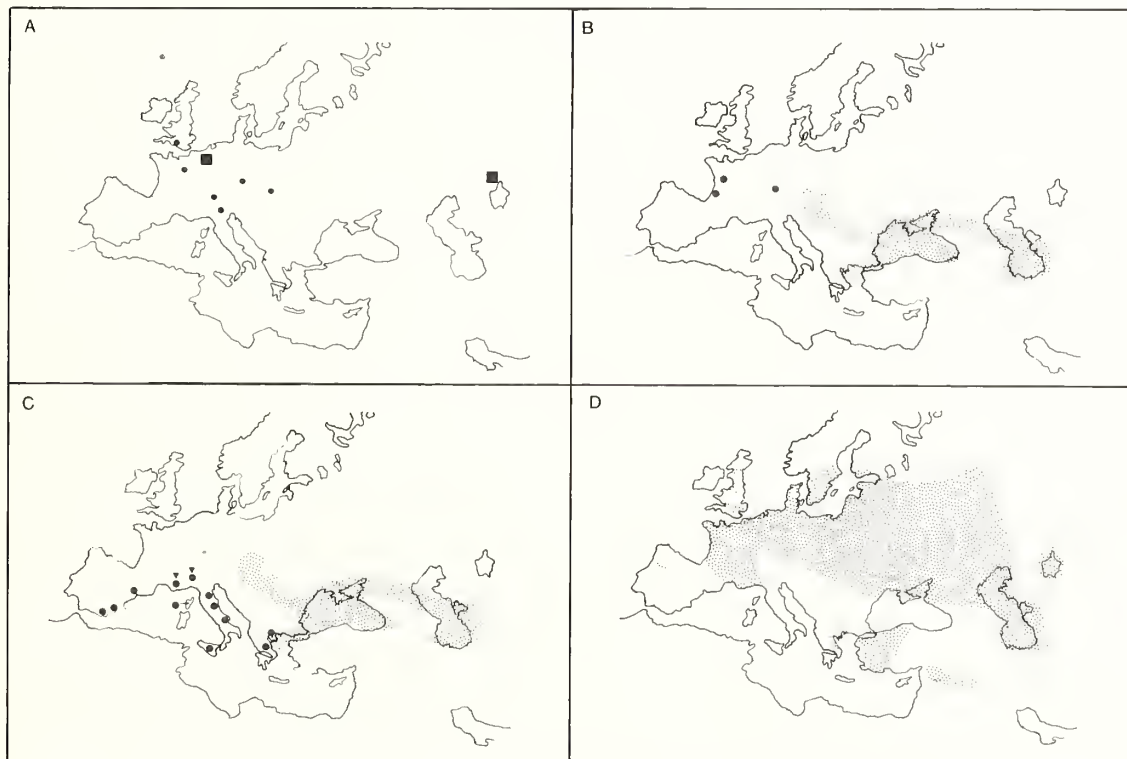
The classifications set out by Keen *in* Moore (1969), by Babak (1983, p. 60) and that proposed herein may be compared in Table 1. So little is known about *Prodreissensia*, based on poorly preserved material, that it is idle to speculate on its relationship with the other genera. Its Palaeogene age, however, does suggest that it is either synonymous with, or an early offshoot from, *Mytilopsis*, if indeed it is a member of the Dreissenidae. Keen's placement of *Dreissenomya* and *Sinucongeria* as subgenera of *Dreissena*, on the grounds that they lack the apophysis, is not accepted. It is, however, worth remembering that all three were probably derived from species of *Mytilopsis* living at more or less the same time and place: the late Miocene of the Paratethys. Babak's classification is an emended version of that proposed by Starabogatov (1970).

The stratigraphic ranges of genera are summarized in Text-fig. 1. Only the two surviving genera, *Mytilopsis* and *Dreissena* are comparatively long-ranging. The remainder are confined to the Paratethys during the Neogene and have short ranges: it is estimated that none survived beyond 5 million years, and that *Dreissenomya* (s.s.) may have existed for as little as 2 million years.

Similarities in shell structures (Taylor, Kennedy and Hall 1973) provide strong evidence that the Corbiculacea and Dreissenacea shared common ancestry. No early Tertiary fossils showing intermediate characters have been found.

There are two possible and inter-related explanations. First, the changes from a shallow infaunal to byssally attached epifaunal mode of life could have occurred quite rapidly. The later sudden radiation shown by the superfamily in the late Miocene of the Paratethys, including re-adaptation to an infaunal mode of life by *Dreissenomya*, suggests that such an explanation is plausible. Although *Mytilus* has small, crenulate, dysodont teeth (Nuttall, fig. 46, 5 in Moore, 1969) situated at the anterior extremity of the shell, loss of dentition in dreissenids may well be connected to the adoption of a heteromyarian, mytiliform shell suitable for epifaunal life. The narrow, pointed, umbonal region allows little space for hinge teeth, whose efficiency would be likely to be very limited in such an anterior position. In addition, the possession of a ligament analogous to that of *Mytilus*, which Trueman (p. N64 in Moore, 1969) described as being among the most powerful known, may also reduce the need for dentition.

The second possible explanation is that, as a general rule, the fossil record of freshwater and marginal marine faunas is far less continuous than those of shelf seas. In the late Cretaceous and Palaeogene of Europe, there were no extensive freshwater basins of comparable extent to the Neogene Paratethys.



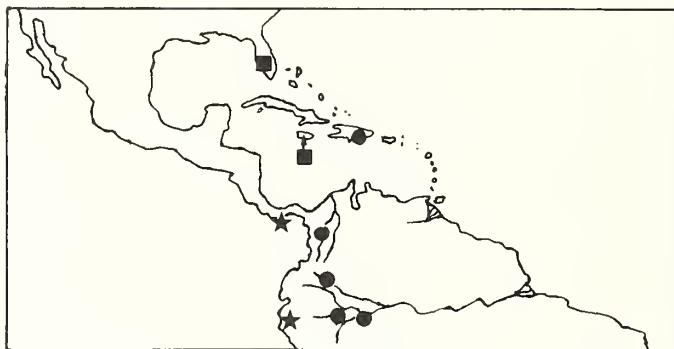
TEXT-FIG. 4. A. Palaeogene distribution of *Mytilopsis*. Key: circles, Eocene, squares, Oligocene. B. Lower and Middle Miocene distribution of *Mytilopsis* in Europe and western Asia. Key: circles, western Europe; stipple, throughout Paratethys. C. Late Miocene (Messinian) distribution of Dreissenacea in Europe and western Asia. Key: circles, *Dreissena*; triangles, *Mytilopsis*; stipple, Paratethys with *Mytilopsis* and *Dreissena* throughout; *Dreissenomya* and *Dreissenomya* (*Sinucongeria*) mainly in western and central areas. D. Recent world distribution of *Dreissena*, shown stippled.

Mytilopsis sowerbyi (d'Orbigny) the only known English Caenozoic species of Dreissenidae occurs quite commonly in freshwater horizons of the English Priabonian Headon Beds, but these beds are confined to comparatively small areas in Hampshire and the Isle of Wight. This sporadic distribution pattern is repeated elsewhere throughout most of the Tertiary (text-fig. 4). *Mytilopsis brardi* (Brongniart), accompanied by small hydrobiid snails, crowd some bedding planes in freshwater Oligo-Miocene deposits of the Mainz Basin of Germany. Glibert and de Heinzelin (1954, pp. 388–9) found only 54 individuals of *M. nystiana* (d'Orbigny) among 90,000 specimens from two marine horizons in the Belgian Lower Oligocene. Most of the other rarities were also non-marine species. Similarly, *M. basteroti* (Deshayes) is a comparatively rare constituent of the rich marine inshore faunas of the Lower Miocene in the Aquitaine Basin, occurring at localities thought to have been situated only a few kilometres from the then shoreline. All the specimens of this species that I have examined are more worn than those of marine species in these faunas, suggesting transport after death (pl. 5, figs. 8–10). The genus occurs in much the same way in the Middle Miocene Faluns of Touraine.

Recognition of chance invasions and local extinctions is of importance in interpreting the history of the superfamily. Such events include:

1. The invasion by *Mytilopsis* of tropical America by the late Oligocene (text-fig. 5), some thirty million years after its first appearance in Europe, probably as adult shells attached to logs, rather than as veliger larvae.

TEXT-FIG. 5. Fossil occurrences of *Mytilopsis* in western Hemisphere. Key: stars, late Oligocene; circles, Miocene; squares, Pliocene.

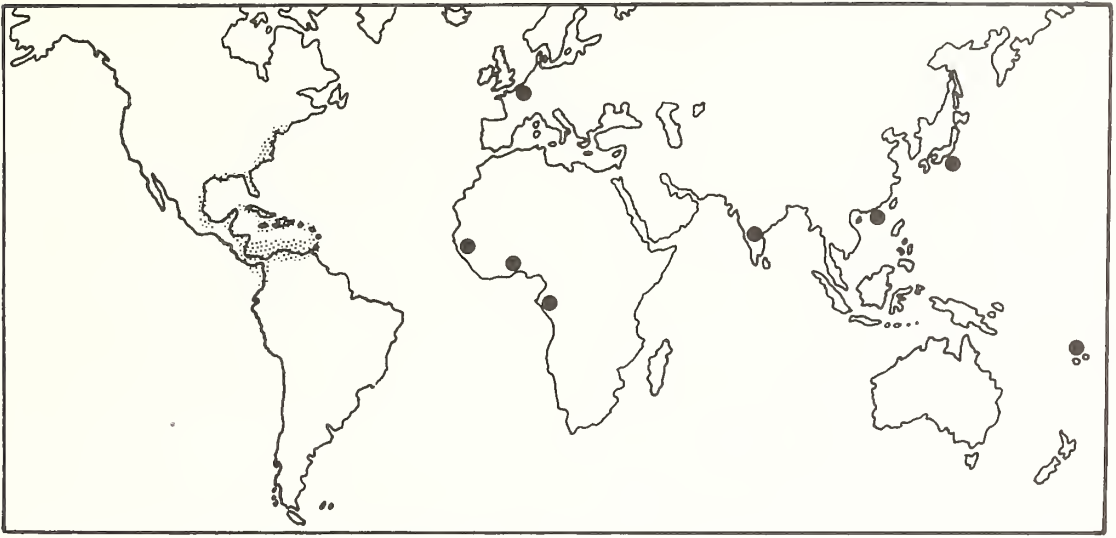


2. The local extinction of *Mytilopsis* in western Europe during the Middle Miocene, preceding its eventual disappearance from the Paratethys.

3. The short-lived invasion, during the Messinian, of the Mediterranean region from the Black Sea, by Paratethyan species of both *Mytilopsis* and *Dreissena* (*Pontodreissena*). Although *Mytilopsis* survived well into the Kimmerian (Lower Pliocene) in the eastern Paratethys and *D. (P.) rostriformis* is still living there, neither is represented by descendants in the western European Pliocene and Pleistocene. As neither genus survived along the borders of the Mediterranean, their disappearance is unlikely to have been due to competition between them. It seems far more likely that their local extinction was due to the removal of suitable fresh and brackish-water habitats.

4. The Recent considerable extension of the geographical distribution of dreissenids as a result of human activity. The industrial revolution, linking of waterways and increase in water-born trade appears to be responsible for the invasion of much of Europe, via the Danube, since the mid-eighteenth century. It is suggested that *Mytilopsis* probably increased its range from Florida northwards along the United States eastern seaboard in similar fashion, whilst shipping has led to its appearances in Fiji, India, Hong-Kong, Japan, West Africa and the Rhine-Scheldt delta (text-fig. 6).

Offshore marine molluscs occupy an extremely stable environment in comparison to the habitats of freshwater molluscs. The history of the Dreissenidae illustrates the success of the highly



TEXT-FIG. 6. Recent distribution of *Mytilopsis*. Key: stipple, naturally occurring; black circles, presumed introduced.

conservative but, most importantly, salinity-tolerant *Mytilopsis* which has survived since the early Tertiary. Nevertheless, its invasion of the Western Hemisphere during the Oligocene appears to have been chance, whilst its disappearance from Europe (except by re-introduction) shows its vulnerability to changed conditions. The rapid diversification of the family in the Paratethys during the late Miocene when *Dreissena*, *Congeria* and infaunal *Dreissenomya* all appeared, is a startling example of fast evolution. The equally rapid extinction of all but *Dreissena* as conditions changed with the break-up of Paratethys shows how vulnerable freshwater molluscs can be when their habitats are altered. Both *Mytilopsis* and *Dreissena* appeared to colonize new regions very slowly unless influenced by man. This inability to spread quickly in natural freshwater conditions is another source of long-term vulnerability. The veliger larva, which allows rapid dispersal in the sea, and even in estuarine conditions successfully exploited by *Mytilopsis*, is still of some advantage in lakes. However, in stretches of river unaffected by tides, veligers are unlikely to be nearly as successful in migrating upstream as the unionacean glochidian larvae attached to the gills of fish.

Acknowledgements. I am indebted to Dr D. Kadolsky (Texaco, London) for first drawing my attention to the work of Andrussov (1897–8). I would like to thank my colleagues at BM(NH), in particular Dr N. J. Morris (Palaeontology) and Dr J. D. Taylor (Zoology) for helpful discussions, Mr R. Croucher, Palaeontology Laboratory for his dissections of very fragile *Dreissenomya* and *Simucongeria*, and members of the photographic studio who were responsible for all the illustrations other than S.E.M. pictures, taken by myself. Finally, I would like to acknowledge my appreciation of the late Dr Myra Keen, one of the group of major contributors to the bivalve volume of the *Treatise on Invertebrate Paleontology*, without whose efforts that work would never have been completed.

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Typescript received 16 January 1989

Revised typescript received 24 November 1989

PREDATION ON *KOSMOCERAS* BY SEMIONOTID FISH IN THE MIDDLE JURASSIC LOWER OXFORD CLAY OF ENGLAND

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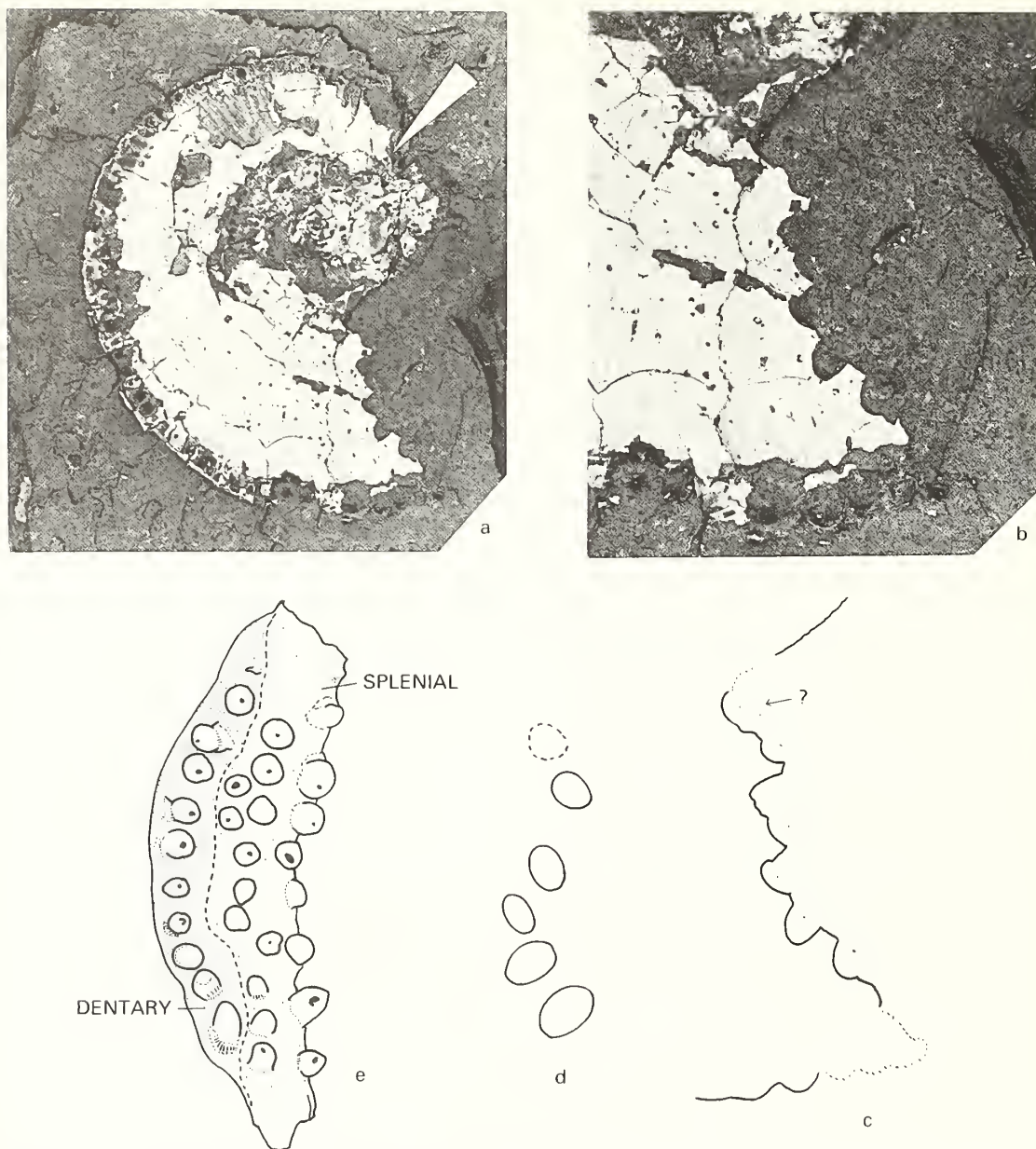
ABSTRACT. Broken ammonite debris is common in the Lower Oxford Clay and is thought to be attributable in part to the activities of predators. A new specimen of *Kosmoceras* (*Zugokosmoceras*) cf. *obductum* (Buckman) displays a series of bite marks in the region of the peristome suggestive of the dentition of the fishes *Lepidotes*, *Heterostroplus* (Semionotidae) and *Mesturus* (Pycnodontidae).

THE ammonite fauna of the Lower Oxford Clay (Middle Callovian, Middle Jurassic) of Peterborough, Cambridgeshire, UK, is remarkable for its exceptional preservation. Although specimens are usually crushed flat, most are preserved in original iridescent white aragonite (Callomon 1968). Species of *Kosmoceras* are most abundant, and include both macroconch and microconch morphs. Many are intact to the peristome, and specimens with extended and complete lappets are numerous. Besides numerous species of *Kosmoceras*, there are also *Eryuoceras* spp., *Binatasphinctes* spp., *Choffatia* sp., *Reineckia* sp., *Hecticoceras* spp. *Sigaloceras* sp. and *Pseudocadoceras* sp. Many of the ammonites are complete, but broken ammonite shell material also occurs in quantity. Shells of the various species of *Kosmoceras* are thin and delicate, and could easily be broken by continued current or storm activity. However, ammonite tests found in storm generated shell beds are often intact and have suffered little from abrasion, suggesting that they are more robust than would at first appear. Much of the broken ammonite debris found must therefore be attributable to the activities of predators rather than to non-biological processes.

DESCRIPTION

The new specimen is a small, laterally compressed phragmacone of *Kosmoceras* cf. *obductum* (Buckman) (text-fig. 1), with the major portion of the body chamber, and a scallop-shaped margin on a slightly damaged peristome. The shell is well preserved, consisting of iridescent white aragonite with a purple sheen. The maximum diameter at the aperture is 50 mm. The specimen was discovered in olive brown bituminous shales at the base of the *K. obductum* Subzone of the *E. coronatum* Zone, at the Dogsthorpe Brick Pit, near Peterborough (Grid reference TF 219019). The specimen has now been protected by a coating of polyvinyl butyral, and is deposited in the collection of the Department of Geology, University of Leicester, accession number LEIUG 99163.

The damaged peristome displays five arcuate incisions, arranged in a semicircle. Each incision is separated by an arc of 3–5 mm from its neighbours. The margin of one incision flaked away after the specimen was collected, reducing the visual impact of the specimen. The incisions have an estimated average diameter of approximately 3 mm, but the shape if complete would have been oval, rather than circular. The arrangement of these incisions is similar to the distribution of teeth (text-fig. 1e) on the dentary of the ganoid fishes *Lepidotes* and *Heterostroplus* (Semionotidae) and possibly the maxilla of *Mesturus* (Pycnodontidae).



TEXT-FIG. 1. *a-d*, *Kosmoceras* cf. *obductum* from the Lower Oxford Clay, Peterborough, with bitten peristome. LEIUG 99163. *a*, phragmacone and body chamber with predator damaged peristome; arrow indicates end of phragmacone, $\times 1.5$. *b*, detail of peristome, approximately $\times 3.5$. *c*, outline of bitten peristome with position of teeth incisions indicated, $\times 3.5$. *d*, position of five teeth which made contact with the ammonite test, $\times 3.5$. *e*, occlusal surface of right lower jaw (here reversed to simulate left jaw) of *Lepidotes macrocheirus*, BM(NH) P6839, Lower Oxford Clay, Peterborough, $\times 3$.

AMMONITE PREDATION

Predation on ammonites has been described by a number of authors (see Lehmann 1976 for a review). Ample evidence that ammonites were victims of predators exists in the form of broken, bitten and damaged tests, but it is often difficult to identify the predators with certainty. Arthropods have been considered to be predators on some Lower Jurassic ammonites, while Kauffman and Kesling (1960) have demonstrated predation by the marine reptile *Mosasaurus*. Small ammonites have been recorded from coprolitic material attributed to plesiosaurs (Wetzel 1960).

Potential predators of ammonites in the Lower Oxford Clay can be found amongst both vertebrates and invertebrates. The large number of belemnites of considerable size (guards up to 30 cm) might be candidates for ammonite predators, as may some of the arthropods. The vertebrate fauna of the Lower Oxford Clay includes a rich diversity of marine reptiles and fishes, but it is only the fishes which have dentitions modified to any degree for coping with hard shell material.

The fish fauna of the Lower Oxford Clay formed the subject of numerous papers by Woodward (1888, 1892*a, b*, 1893, 1896, 1928, 1929), but has received little attention since. Fortunately the dentitions of many of the numerous taxa are available for analysis, most housed in the British Museum (Natural History).

Among the fish with durophagous dentitions are the ganoid fishes *Lepidotes* and *Heterostrophus* [= *Dapedium*?] (Semionotidae), *Mesturus leedsi* Woodward (Pycnodontidae), the hybodont shark *Asteracanthus ornatissimus* Agassiz (Hybodontidae), and the chimaeroids *Brachymylus*, *Pachymylus* and *Ischyodus*. The dentition of the chimaeroids is robust, and incorporates large tritoral areas designed to crush shell material. Their sharp mandibular dental plates may have been used to dig for shelled prey. These teeth are unlikely to leave scallop-shaped incisions on any invertebrate test. The dentition of *Asteracanthus* is complex, and comprises a highly heterodont assemblage, although most teeth comprise a broad tritoral area with a well developed central ridge. It is unlikely that *Asteracanthus* would have been capable of producing a crescentic series of incisions. The dentition of the pycnodont *Mesturus* consists of robust, rounded teeth, often with tritoral cusps. Teeth on the splenial and vomer of *Mesturus* are arranged in straight rows (Woodward 1896), and would not produce a crescent-shaped bite. There are four teeth on each premaxilla and dentary of *Mesturus*. They are directed forward and have expanded occlusal surfaces ideal for nibbling small shelly organisms. This dental pattern could produce the pattern of bites seen in the ammonite if all premaxillary teeth from one side, plus one of the premaxillary teeth from the other side of the jaw had made contact with the ammonite test. The dentitions of *Heterostrophus phillipsi* Woodward, 1928, and the three species of Lower Oxford Clay *Lepidotes* (*L. leedsi* Woodward, 1895, *L. macrocheirus* Egerton, 1845 and *L. latifrons* Woodward, 1893) are robust, sometimes peg-like with slightly expanded tips, and well-spaced along the jaw. The dentary is crescentic in occlusal view. Any of these four species could have produced the crescentic bite seen in the ammonite (text-fig. 1*e*).

Alternatives to fish predators are difficult to find preserved as macrofossils in the Lower Oxford Clay. Two arthropods, *Mecochirus* and *Goniochirus*, are common in the same bed from which the ammonite was collected, but both have rather small claws, and those of *Mecochirus* are extremely elongate and delicate, and appear somewhat specialized. Other cephalopods, especially the various naked forms, were possible predators on ammonites, but details of the jaw apparatus in these are poorly known.

DISCUSSION

Lepidotes spp. and *Heterostrophus phillipsi* are the most likely candidates for producing the damaged peristome of the ammonite, but *Mesturus leedsi* cannot be ruled out. *Lepidotes* and *Heterostrophus* are common in the Lower Oxford Clay, but *Mesturus* appears to be rare. Complete specimens are not common, but isolated scales are very abundant. *Lepidotes* is possibly the most abundant large fish in the Lower Oxford Clay, but this is difficult to assess as the robust enamel scales are easy to detect, and have a relatively high preservation potential. No information is available on the level at which *Lepidotes* spp. or *Heterostrophus* lived in the water column, but their

general robust fusiform shape, and the massive form of the skull might suggest that they were part of the near benthos biota rather than a part of the surface living community. Perhaps ammonites were also part of the benthic community.

The trophic status of a number of vertebrates from the Lower Oxford Clay has been discussed by Martill (1985, 1987, 1988), but as yet no single account of the interrelationships of the biota is available. This stems mainly from a lack of reliable data. The top of the food chain was dominated by the giant carnivorous reptiles *Liopleurodon* and *Phiosaurus*. There were a number of opportunistic feeders, including the marine crocodilian *Metriorhynchus* which fed on giant fish and hooked cephalopods (Martill 1987). Many of the vertebrates were highly specialized feeders; the ichthyosaur *Ophthalmosaurus* is thought to have fed exclusively on naked cephalopods, while the marine crocodile *Steneosaurus* and the long necked plesiosaurs were probably mainly fish and naked cephalopod feeders. The fish fauna displays similar trophic niche partitioning. The giant pachycormid *Leedsichthys* was a plankton feeder (Martill 1988), while the other pachycormids *Hypsocormus* and *Asthenocormus* were active predators on smaller fish. Clearly the Lower Oxford Clay food web was highly complex.

Acknowledgments. Thanks go to the London Brick Company for permission to visit the Dogsthorpe Brick Pit, to Alan Dawn for help in excavating the site, and to Colin Patterson (BMNH) for permission to examine material in his care.

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Typescript received 12 June 1989

Revised typescript received 31 July 1989

NON-PREDATORY DRILLING OF MISSISSIPPIAN CRINOIDS BY PLATYCERATID GASTROPODS

by TOMASZ K. BAUMILLER

ABSTRACT. The conical hole in the tegmen of a Mississippian crinoid (*Macrocrinus mundulus*) directly underneath the shell of a platyceratid gastropod, *Platyceras* (*Orthonychia*) sp., and similar holes in other Mississippian crinoids (*Batocrinus irregularis* and *B. icosidactylus*) demonstrate the drilling abilities of platyceratids. This is the first case of drilling by an archaeogastropod. Drilling on the crinoid host by the gastropod was non-predatory; the relationship was probably parasitic. This study, the first to identify unequivocally a Palaeozoic borer, supports the notion that gastropod drilling has evolved several times.

EVIDENCE implying predation on Palaeozoic invertebrates is well documented (Fenton and Fenton 1931; Brunton 1966; Rohr 1976; Ausich and Gurrola 1979). Examples include conical holes, mostly in brachiopods, which have been attributed to Palaeozoic gastropods because of their similarity to drillholes produced by Recent predatory gastropods (Cameron 1967; Sheehan and Lespérance 1978; Smith *et al.* 1985). This interpretation is not universally accepted, since the Palaeozoic taxon responsible for them has not been conclusively identified (Carriker and Yochelson 1968; Sohl 1969). The discovery of a borehole in a Mississippian crinoid, directly beneath an attached platyceratid gastropod, is the first definitive demonstration of drilling activity by a Palaeozoic gastropod.

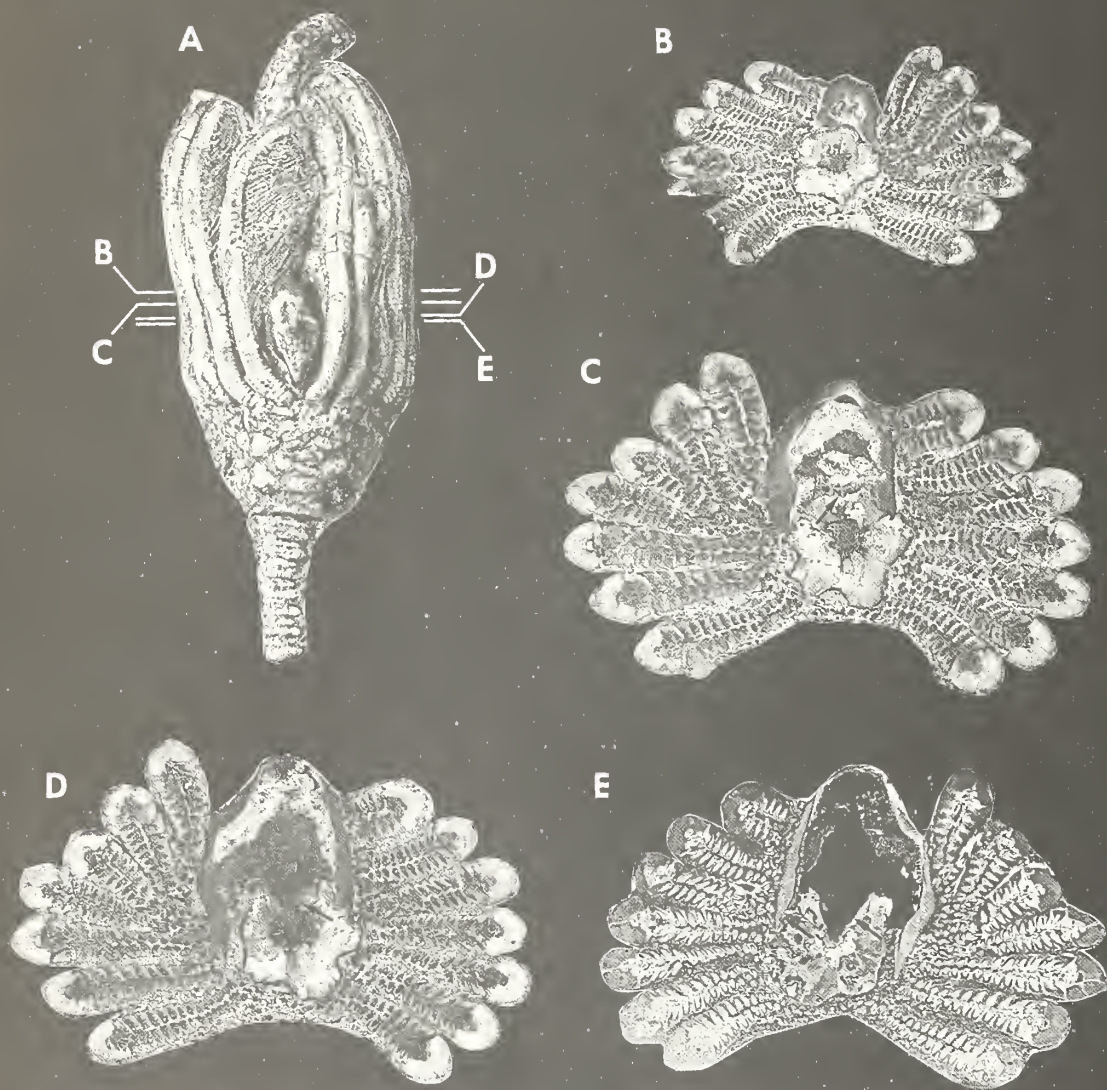
PLATYCERATID-CRINOID INTERACTION

The archaeogastropod family Platyceratidae (Knight *et al.* 1960) is well known for its association with crinoids (Meyer and Ausich 1983). Generally, the gastropod is firmly attached to the crinoid calyx usually above the base of the arms. Its position, commonly covering the crinoid anus, and the close conformity of its margin to the morphology of the calyx, has suggested commensalism and that platyceratids were coprophages on crinoid wastes (Keyes 1890; Bowsher 1955). Recently it has been argued that platyceratids were parasites feeding on crinoid gametes (Lane 1984). The parasitic interpretation is supported by the smaller size of gastropod-infested crinoids as compared to uninfested ones (Rollins and Brezinski 1988).

Commonly, the gastropod sits directly over the crinoid anus, which is flush with the tegmen, or upper portion of the calyx. However, several platyceratids have been found situated on the crinoid tegmen but well away from the anus (Lane 1978). In such instances the infested crinoids have a long stout anal tube, with the anus at its apex, while the platyceratid rests at the base of the tube. In this position the gastropod could not extract anything from the crinoid without drilling into the host. Therefore, to test the hypothesis that platyceratids were capable of boring their tube-bearing hosts, I serially ground a crinoid with *Platyceras* (*Orthonychia*) sp. at the base of its long tube.

PLATYCERATID DRILLHOLES

In the collections of the Field Museum of Natural History (FMNH) I found a well-preserved specimen of *Macrocrinus mundulus* (Batocrinidae) with a species of *Platyceras* (*Orthonychia*) at the base of the anal tube. Specimen P. 19426, which was collected at Canton, Indiana, USA, from rocks of Tournaisian age, was ground perpendicular to the oral–aboral axis (long axis of the anal tube)



TEXT-FIG. 1. Specimen of *Macrocerinus mundulus* (FMNH P.19426) with a long anal tube and *Platyceras* on its tegmen. (A) Lateral view of specimen with lines B, C, D, and E indicating positions at which photographs B, C, D, E of ground sections were taken. Ground surfaces are perpendicular to the plane of the page and the long axis of the specimen, $\times 1.4$. (B) Section through the arms, anal tube and the anterior of the *Platyceras*. Note that the anal tube plate directly beneath the platyceratid appears intact, $\times 3.0$. (C) Section 1.0 mm below B. Arrow points to a small concavity in the anal tube plate beneath the platyceratid, $\times 3.0$. (D) Section 1.0 mm below C. Arrow points to drill hole. Note contrast between hole filled with dark matrix and light colour of anal tube plates, $\times 3.0$. (E) Section through centre of drill hole. Note that hole penetrates to centre of anal tube and the tight fit between the test of gastropod and the anal tube, $\times 2.9$.

at 0.5 to 1.0 mm intervals, starting at the apex of the tube (text-fig. 1). The serial sections revealed a circular, conical hole (3 mm outer diameter) beneath the central, anterior portion of the gastropod shell. The hole is easily recognized from the colour contrast between the white plates of the anal tube and the red matrix filling the body cavity of the gastropod and the hole underneath it.

In addition, 27 specimens of Visean *Batocrinus icosidactylus* and *B. irregularis* from the collections of the Field Museum and Indiana University, Bloomington, USA, also possessing a long anal tube, were found with previously undescribed holes in their tegmina. The location of these holes is highly stereotyped: they are either just below or at the base of the anal tube (text-figs. 2 and 3). The holes also exhibit little variation in morphology; they are round in plan view, cylindrical to conical in cross-section, with a mean outer diameter of 2.2 mm (range from 1.4 to 3.2 mm) (text-fig. 2H). The morphology and position of these holes match those of the hole in *Macrocrinus* beneath *Platyceras* (text-figs. 1E, 2H).

Platyceratids occur with the aforementioned batocrinids in localities of the Salem Limestone (Cummings *et al.* 1905), a fact consistent with the interpretation that these gastropods were responsible for the drillholes. The lack of an association between *Platyceras* and *Batocrinus* in these localities may be a taphonomic artifact. When platyceratids are associated with crinoid tegmina, articulated crinoid arms are also preserved. This implies either that the arms prevented the post-mortem separation of the two organisms or that the process leading to the disarticulation of the arms from the crown also led to the detachment of the gastropod from the crinoid. *Batocrinus* with preserved arms have not been described. The absence of platyceratids on *Batocrinus* is thus not inconsistent with this mode of preservation.

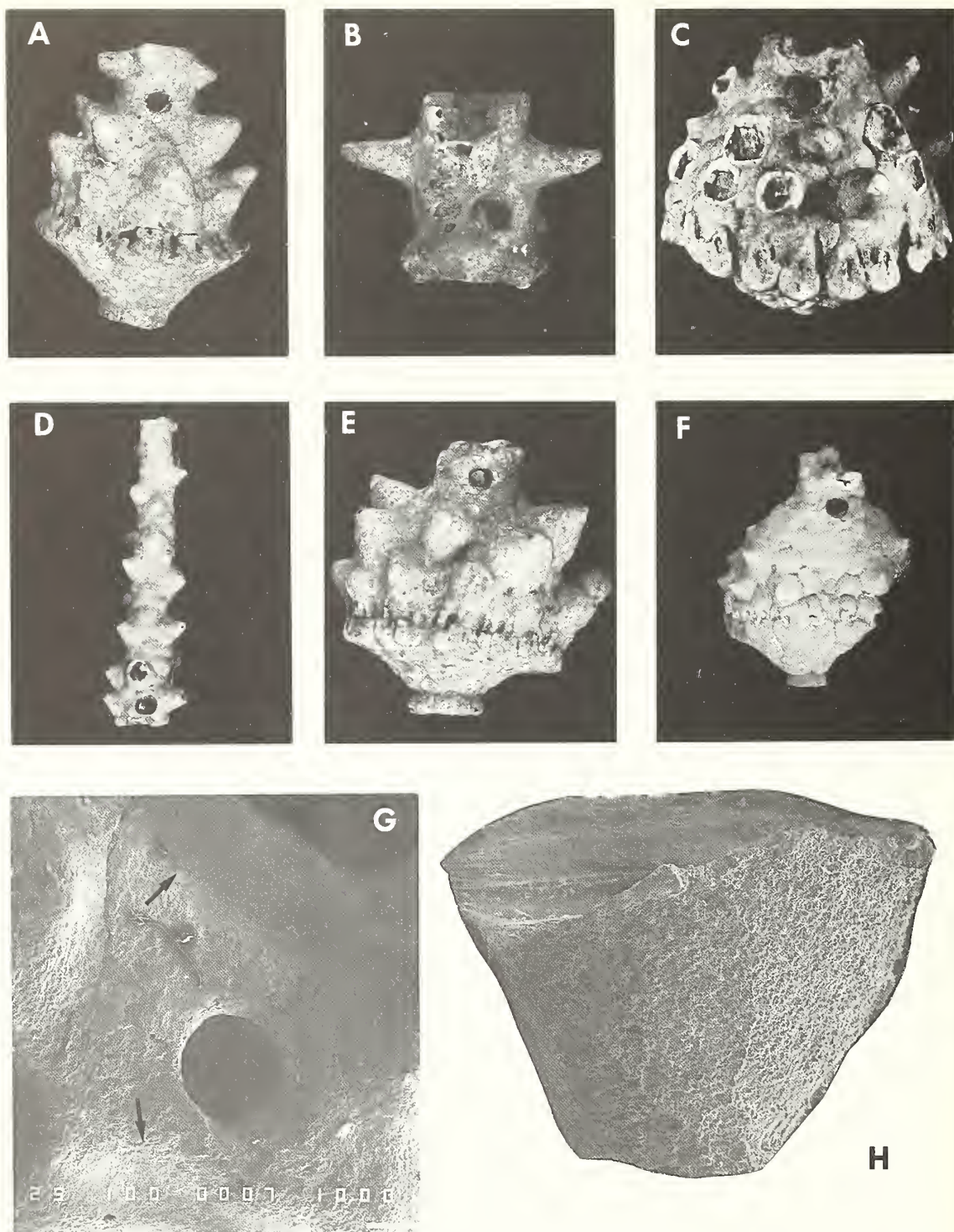
These results establish the boring abilities of the Mississippian *Platyceras* (*Orthonychia*), the first unequivocal example of a drilling Palaeozoic gastropod.

DISCUSSION

Non-predatory nature of drillholes

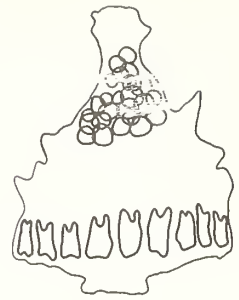
The boring by *Platyceras* does not necessarily imply predation on the crinoid. Several lines of evidence suggest that the relationship was non-predatory. The tight fit between the margin of *Platyceras* and the tegmen of *Macrocrinus* (text-figs. 1D, 1E), U-shaped attachment scars surrounding the boreholes (text-fig. 2G), instances of multiple boreholes, and healed (or incomplete) boreholes on *Batocrinus* all indicate that the association was long term and that drilling was not fatal to the crinoid. Furthermore, Recent parasitic capulid gastropods, which have a shell morphology very like the platyceratids, also drill their host (Orr 1962; Kosuge and Hayashi 1967).

Whether this relationship was beneficial, neutral, or detrimental to the crinoid cannot be determined conclusively. Although drilling itself was probably detrimental, the feeding strategy of platyceratids is most relevant in distinguishing between the three alternatives. If the gastropods fed exclusively on crinoid wastes, then their position at the apex of the anal tube, directly over the crinoid anus, would have sufficed. It is possible, however, that these relatively large gastropods would have been unstable in this position due to the small size of the distal end of the tube. Drilling at the base of the tube would have permitted feeding in a more stable orientation. More probably the gastropod extracted from the crinoid more than just waste matter. Camerate crinoid food grooves converge subtegminally and carry within them food particles collected by the dense filtration fans. By inserting its snout into the tegmen the gastropod could have extracted food from these grooves. This would have involved penetrating the crinoid gut wall, since in camerates the subtegminally food grooves form closed tubular conduits leading directly to the fore-gut (Haugh 1975); a similar situation has been described for the parasitic prosobranch, *Echineulinia*, whose proboscis was found to pierce the intestinal wall of its host echinoid (Lützen and Nielsen 1975). In crinoids without an anal tube this could have been accomplished without drilling, simply by using the existing anal opening through which to insert the snout beneath the tegmen. Such a strategy would not have worked with crinoids possessing a long tube, due to the greater distance of the anus from the food grooves lying deep below the tegmen. Drilling would be essential. This may be an



TEXT-FIG. 2. Drillholes in bactocrinids from the Salem Limestone. (A) *Batocrinus icosidactylus* (FMNH P.19393), $\times 1.9$. (B) Anal tube of *B. icosidactylus* (FMNH P.19392), $\times 2.5$. (C) *B. icosidactylus* (FMNH P.19394), $\times 2.2$. (D) Anal tube of *B. icosidactylus* (FMNH 19394), $\times 1.4$. (E) *B. icosidactylus* (FMNH P.21506), $\times 2.0$. (F) *B. irregularis* (FMNH P.19402), $\times 2.1$. (G) SEM of *B. icosidactylus* (FMNH P.19402). Arrows point to U-shaped scar around hole, $\times 8.8$. (H) A latex cast of drillhole in *B. icosidactylus* (FMNH PE.1957). Orientation of cast is with the top corresponding to the outer surface of the anal tube and the bottom to the inner surface, $\times 2.3$.

TEXT-FIG. 3. A reconstruction of the calyx of *Batocrinus* with part of the anal tube. Actual drillholes projected onto reconstruction. Note stereotypic position of holes.



'arms-race' (Vermeij 1987) in which crinoids evolved an anal tube in response to gastropod parasitism, which in turn led to the evolution of platyceratid drilling. Though highly conjectural, this hypothesis may be tested by determining whether anal tubes evolved preferentially in gastropod-infested lineages, and whether platyceratid drillholes are found in crinoids without anal tubes.

The drilling habit and 'evolutionary radiations'

Other evolutionary implications of the drilling habit of *Platyceras* hinge upon our knowledge of the systematics of this group. Although archaeogastropods are probably not a true clade (Hickman 1988), if the taxonomic scheme proposed by Knight *et al.* (1960) is correct with regard to platyceratids, *Platyceras* represents an example of independent evolution of drilling in gastropods that did not lead to a major diversification (Smith *et al.* 1985; Fürsich and Jablonski 1984). Platyceratid generic diversity did not undergo major changes during or after the Mississippian (Bowsher 1955), and their extinction at the end of the Permian (Bowsher 1955, but see Bandel 1988) coincides with the extinction of other invertebrates, including most of their crinoid hosts.

A pre-Mississippian origin of the platyceratid drilling habit is possible, for platyceratids as well as bored echinoderms are found in rocks of Ordovician to Permian age (Bowsher 1955; Brett 1978; Paul 1971). In most instances, however, these borings are in the form of pits which do not penetrate the skeletal plates of the host echinoderm, and their origin has been attributed to various epizoans. Whether platyceratids were responsible for any of these pits remain to be examined.

It has been argued that evolutionary 'failures' of taxa with drilling abilities resulted either from deterministic causes related to the adaptive value of this innovation (e.g. inability to drill rapidly) or from factors unrelated to the innovation itself but affecting rates of speciation and extinction (Smith *et al.* 1985; Fürsich and Jablonski 1984). The identification of the innovation-bearing taxon provides an excellent opportunity for testing these ideas. Thus the suggestion that the lack of a hard skeleton (Smith *et al.* 1985) contributed to the evolutionary failure of Palaeozoic drillers must be rejected for the shelled *Platyceras*. Furthermore, the non-predatory nature of these drillholes forces us to make a distinction between predatory and parasitic drilling, as well as between their evolutionary implications.

Acknowledgements. I thank M. Foote, D. Jablonski, M. LaBarbera, M. Listokin, D. Miller, M. Nitecki, and an anonymous reviewer for comments on the manuscript, and D. Miller for technical assistance. Partial funding for this project was provided by the Gurley Fund of the University of Chicago.

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Typescript received 19 June 1989

Revised typescript received 18 August 1989

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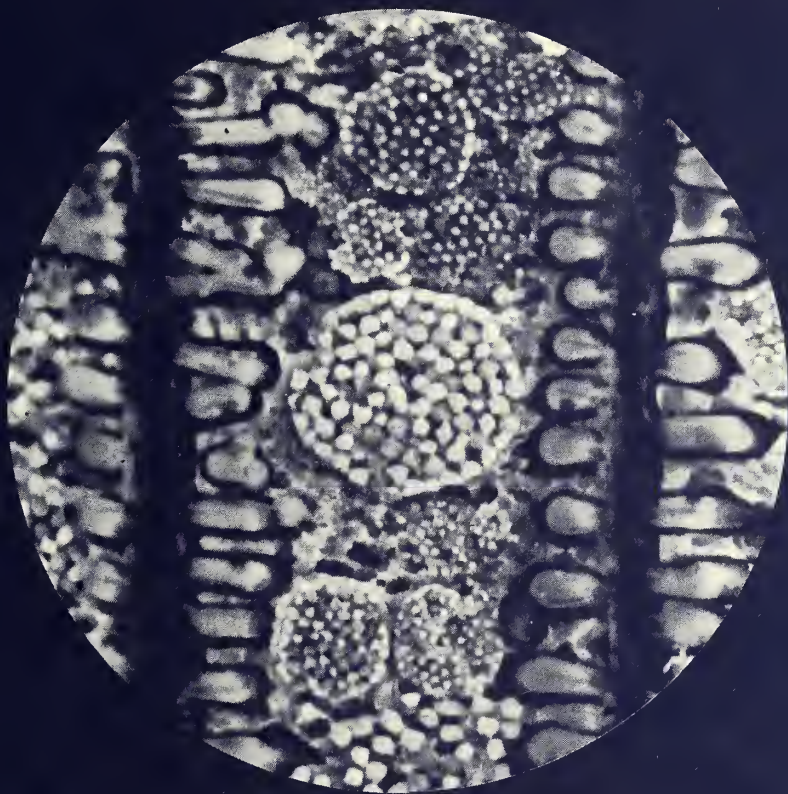
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VOLUME 33 · PART 4 NOVEMBER 1990



Published by

The Palaeontological Association · London

Price £30

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Cover: Framboidal pyrite within lumen of a tracheid of the early land plant, *Gosslingia breconensis*, from the Lower Old Red Sandstone of South Wales. $\times 700$. See P. Kenrick and D. Edwards. *Botanical Journal of the Linnean Society*, 97, 95–123.

BIOMECHANICS OF TRILOBITE EXOSKELETONS

by NADINE V. WILMOT

ABSTRACT. Most skeletal materials, such as bone and insect cuticle, are viscoelastic but heavily mineralized structures such as mollusc shell, are linearly elastic. The type of microstructure used in making a skeleton is related to required mechanical strength and to the metabolic cost involved in construction. The effects of composition, microstructure, and architecture on mechanical properties are discussed, and then related to trilobite exoskeletons. Due to their composition and internal organization, trilobite cuticles can be regarded as ceramics that behaved in a linearly elastic manner. The small size of the calcite crystals and the presence of an organic framework reduced the risk of crack formation and slowed the progress of fractures. As a result of its crystal arrangement, the thin outer prismatic layer would have had good compressive strength, but only poor crack-stopping abilities, whereas the underlying principal layer added bulk to the cuticle and deflected cracks. Structurally, trilobite exoskeletons are analogous to monocoque shells, that is, they are strong 'thin shells' with the same composition throughout and behave as a 'stressed skin'. The overall architecture of the cephalon and pygidium is of a series of modified domes, strengthened by the presence of the doublure, whereas thoracic segments are compromise structures which allow articulation as well as conferring mechanical strength.

THE ways in which materials respond to forces acting upon them are determined by their mechanical properties. Accommodation of the resulting stresses is a function of the composition, microstructural organization, and overall form (or architecture) of the specimen. The study of the mechanical characteristics of biological materials is part of the discipline known as biomechanics, a relatively new field with most research occurring from the 1970s onwards. Such research has concentrated on investigating the biomechanics of Recent skeletal materials such as bone (Currey 1969, 1975, 1979), insect cuticle (Hepburn *et al.* 1975; Vincent 1980), and mollusc shell (Taylor and Layman 1972; Currey and Taylor 1974; Currey 1976, 1980; Jackson *et al.* 1988) in order to compare their competencies. Various mechanical tests have been developed to measure the tensile, compressive, bending, and hardness characteristics of these materials by modification of standard engineering procedures. However, although the tests were basically the same, authors each followed their own individual techniques. Currey (1980) argued that sample preparation, size, and shape, would all have a bearing on the results obtained, and so demonstrated the desirability of a standard methodology.

These studies have demonstrated that not only do materials with the same composition have different mechanical properties, but also that biomechanics may not be the most important factor in their design; the metabolic cost involved in constructing a skeleton is also very important (Currey 1980). Some of the common terms used in biomechanical studies are explained at the end of this section.

The mechanical properties of biological materials have generally been related to composition and microstructure. The significance of the form of the organism has only been studied in depth for the Ostracoda (Benson 1974, 1975, 1981, 1982). Most testing of arthropod exoskeletons has been on insect cuticle, mainly because they are the most common arthropods today (see Vincent 1980 for review). However, such cuticles are uncalcified and behave as viscoelastic materials, in contrast to heavily mineralized exoskeletons which behave as ceramics and are linearly elastic. Consequently the biomechanics of trilobite exoskeletons, which were strongly calcified, are better compared with other mineralized skeletons such as mollusc shells, rather than insect cuticle. In the following sections the effects of composition, ultrastructure, and architecture on mechanical properties are discussed in turn, and the principles involved then related to trilobite cuticles.

Terminology

Stress (σ): force per unit area.

Strain (ϵ): a ratio to express the deformation created within a specimen when subjected to stress. It is the ratio of the change in size to the basic size.

Stiffness is a measure of the resistance of a material to deformation. It is measured by performing tensile tests (Currey and Taylor 1974; Joffe *et al.* 1975; Ker 1980), or compression tests (Taylor and Layman 1972; Currey 1976); both types of test have to be repeatable, that is, not incurring permanent damage to the specimen such as fracture.

Hardness measures the ease with which a material flows under a stress, and is related to the stiffness of the material and its plasticity. For details of tests see Taylor and Layman (1972) and Hillerton *et al.* (1982). It is useful for comparing viscoelastic materials, or ceramics with grain sizes of about 100 μm (Craig and Vaughan 1981).

Linearly elastic materials, such as ceramics, react immediately to the application of a stress, for as long as it is present, and on its removal immediately revert back to their pre-stressed state (Text-fig. 1A (i)). In a linearly elastic material, strain is directly proportional to stress and the stress/strain plot is linear:

$$\epsilon = \sigma/E,$$

where E is a constant (Young's modulus) and is a measure of the stiffness of the material.

Viscoelastic materials, such as insect cuticle, increasingly deform the longer a force is applied. Once the stress is removed, recovery is also gradual, so that any measurement of strain is time-dependent (Text-fig. 1A (ii)).

See Wainwright *et al.* (1976), Dorrington (1980), Gordon (1980), and Vincent (1980, 1982) for more details about linear elastic and viscoelastic materials.

COMPOSITION

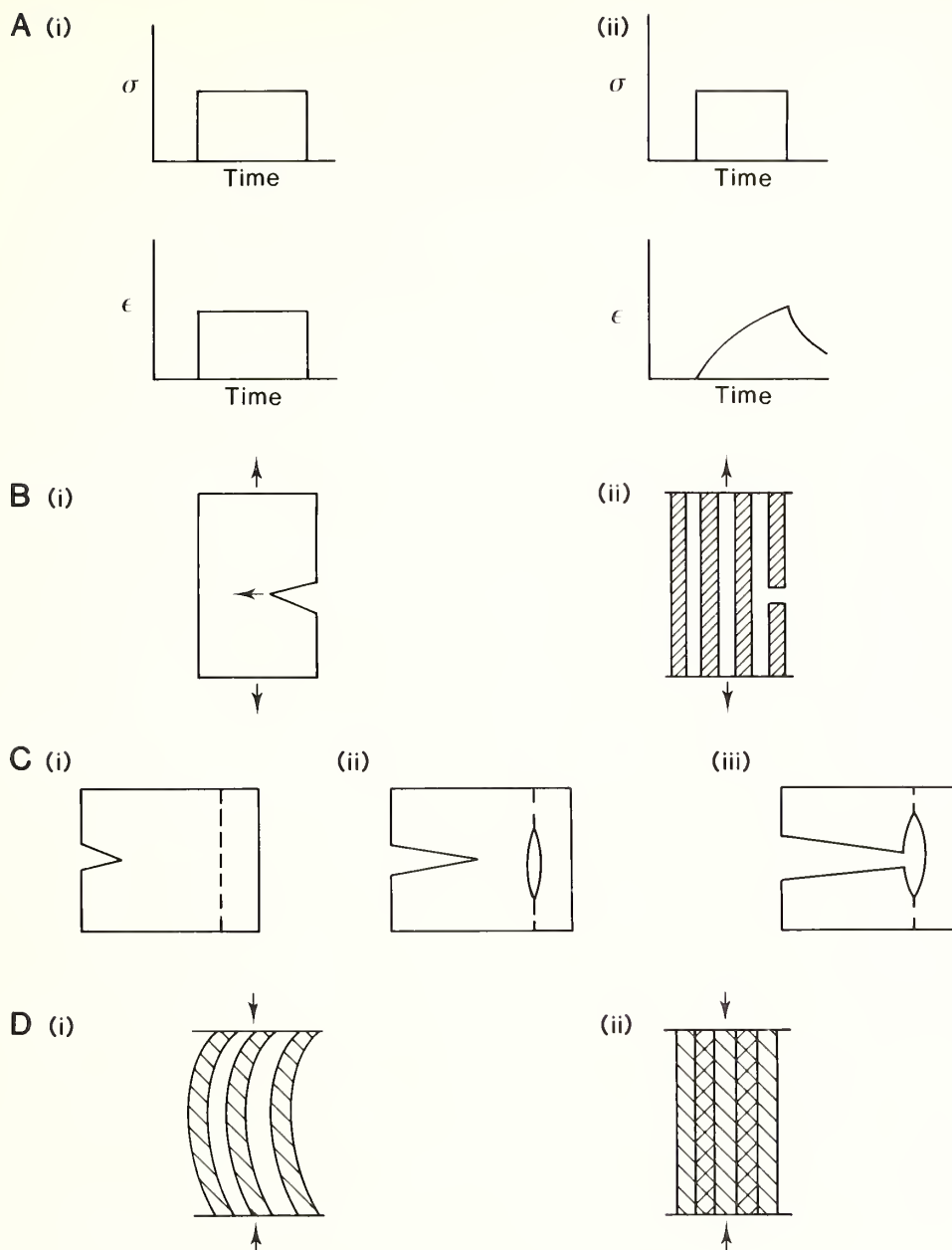
Every material has a unique response to both tension and compression, which is largely due to its composition and the strength of the bonds that maintain its atomic structure. For example, ceramics, characterized by ionic or covalent bonding, have great compressive strength.

Organisms are subject to both tensile and compressive forces, and their skeletons usually comprise a mixture of components, that is, they are composites. Tensile forces usually occur within the structure of the skeleton, or are created by support of the viscera, whereas compressive forces can be induced by walking, the surrounding water pressure, or predation.

Insect cuticle is one of the most efficiently constructed naturally occurring composites, being composed of chitin fibrils weakly bonded to a protein matrix. Chitin is very strong when subject to tensile forces, whereas the type of protein matrix determines stiffness (Hillerton 1984). The arrangement of these two components is also important (see below). Stiff and pliant insect cuticles owe their differences to their protein matrix compositions; the properties of the chitin fibrils are always the same (Hillerton 1984). Additional hardening can be generated by sclerotization, for example in locust incisors (Hillerton 1980). This involves the incorporation of phenols which become tightly bound within the cuticle, coupled with some loss of water (Vincent and Hillerton 1979).

Some marine arthropods harden their exoskeletons by reducing the amount of protein present (compared with terrestrial forms) and mineralizing their exoskeletons with calcium salts. It has been demonstrated for crustaceans that the greater the proportion of calcium salts, the harder the cuticle becomes (Welinder 1974; Abby-Kalio 1982). The type of mineralization is also important, for example the cuticle of the mantid shrimp *Gonodactylus* is mainly composed of calcium carbonate, but the harder outer surface of the smashing limb is predominantly calcium phosphate (Currey *et al.* 1982).

Sometimes organic matter is incorporated within the crystal lattice and alters the way in which



TEXT-FIG. 1. Responses of different materials to stress, based on Wainwright *et al.* (1976, fig. 2. 12), and Gordon (1980, figs 6 and 7). A (i), linearly elastic materials; A (ii), viscoelastic materials. B (i), continuous material is weak in tension, as cracks can advance unimpeded; B (ii), isolated elements are stronger in tension as cracks are unable to spread once the first element has broken. C, weak interfaces prevent the spread of cracks (Cook-Gordon mechanism): (i), crack formation begins; (ii), weak interface opens out in advance of the crack; (iii), progression of the crack is stopped. D, lateral bonds increase compressive strength: (i), isolated elements bend under compression; (ii), weak lateral bonds restrict movement.

the mineral fractures. This is exemplified by proteins within the calcite crystals of echinoderm plates (Berman *et al.* 1988). Although the concentration of protein is very small (only approximately ten molecules per 1×10^6 unit cells) these crystals are less brittle than inorganic calcite.

MICROSTRUCTURE

The size and arrangement of skeletal materials are of fundamental importance to the mechanical behaviour of the structure as a whole. In general, composites are stronger than pure materials. Cracks, generated in tensile conditions, are unable to propagate between isolated elements (Text-fig. 1b), hence chitin fibrils are extremely strong as they are composed of individual long chains of chitin molecules. If one chain is broken, the fracture does not spread to the others.

Weak interfaces within a material can also give strength due to the Cook-Gordon mechanism (Cook and Gordon 1964). As a crack propagates through a material, the weak interface opens up in advance. When the crack reaches the hole, its energy is dissipated and so is unable to continue (Text-fig. 1c). Wood behaves in this manner. Bonding between components can also increase compressive strength by creating greater resistance to bending (Text-fig. 1d).

Arthropod cuticle is a very efficient composite as it contains tension- and compression-resistant members. The chitin/protein fibrils are arranged in sheets parallel to the cuticle surface. Each sheet contains fibrils orientated in the same direction, but successive layers are rotated by a few degrees to produce a helicoidal structure. The typical laminated appearance of arthropod cuticle is due to this internal arrangement; each unit of 180° rotation of the helicoid corresponding to a single lamina (Bouligand 1965; Neville and Luke 1969; Neville 1970; Livolant *et al.* 1978). Consequently the cuticle is strong in tension along any plane parallel to the surface. Sometimes the sheets show preferred orientation along the direction of greatest stress (Wainwright *et al.* 1976), for example in the walking legs of spiders (Barth 1973), the hind limbs of coleopterans (Dennell 1978), the pedipalps of scorpions (Mutvei 1977; Dalingwater 1980), in *Limulus* cuticle (Mutvei 1977; Dalingwater 1980), and the legs of the Carboniferous eurypterid *Mycterops* (Dalingwater 1985). In such cases the cuticle is very strong along the plane of preferred fibre orientation but much weaker in other directions (Harris 1980).

The organic matrix of heavily mineralized skeletons is one of the most important factors in determining its mechanical properties. Most biomineralization is an 'organic matrix-mediated' process (Lowenstam 1981) where the organic matter forms a framework not only to control the nucleation, size, and orientation of the inorganic crystals, but also the physical behaviour of the shell (Krampitz *et al.* 1983). The organic matrix of crustaceans is a chitin-protein complex, and the proteins can be subdivided into water insoluble, and soluble fractions (Richards 1951) which are species-specific (Hackman 1974). This is also true in other marine invertebrates such as molluscs. Weiner *et al.* (1983) demonstrated that molluscan insoluble matrix (including chitin fibrils) forms a framework to limit the size and orientation of the crystals, which is very important mechanically, and also supports the soluble matrix that controls nucleation sites (see also the review by Mann 1988 concerning organic matrices).

The quantity and mechanical characteristics of the organic framework compared with the crystalline component can greatly influence the strength of a 'stony' (Wainwright *et al.* 1976) skeleton. As the matrix is much less brittle than the crystals it encloses, when sufficiently thick it can absorb some of the energy involved in crack propagation by plastic flow. If the organic matrix is thin, fractures are prevented from developing mainly by deflecting cracks as they reach crystal boundaries.

The size of the crystalline component of a stony skeleton (as controlled by the organic framework) is also very important. The larger the component, the more likely it is to contain flaws such as internal deformation or cracks. For linearly elastic solids at a given stress level, there is a 'critical crack length' or defect size at which fracture occurs. Hence it is advantageous for a ceramic to be constructed from small components to reduce the chances of containing defects. For calcium carbonate minerals in tension at 50 MN m^{-2} and 100 MN m^{-2} , the critical crack length is $2\text{--}8 \mu\text{m}$

(Wainwright *et al.* 1976). In general, heavily mineralized skeletal materials have grain sizes with one dimension smaller than $3\text{ }\mu\text{m}$ which minimizes fracture occurrence. Uniformity in size is also advantageous, to prevent weak links generated by larger components. The less organic matrix present, the more important it is for the crystal sizes to be small, so that if cracks do form, they frequently have to change direction at crystal boundaries: a process that requires additional energy. Hence fine-grained ceramic skeletons that contain only a small amount of organic matrix, are much stronger than a large inorganic crystal. This has been demonstrated for mollusc shells, which contain only 0.1–5% matrix (Currey 1980) and yet are stronger than inorganically precipitated calcite (Taylor and Layman 1972). Currey (1980, fig. 5) has illustrated the extremely good crack-stopping capabilities of molluscan nacre, which is composed of many thin sheets of aragonite separated by thin organic layers. A crack has to proceed along a very tortuous path in order to cross this type of microstructure. Therefore it is not surprising that most ceramic skeletons are fine grained and contain very few voids. When voids do occur, such as ducts, their function outweighs the structural weaknesses they induce (Wainwright *et al.* 1976).

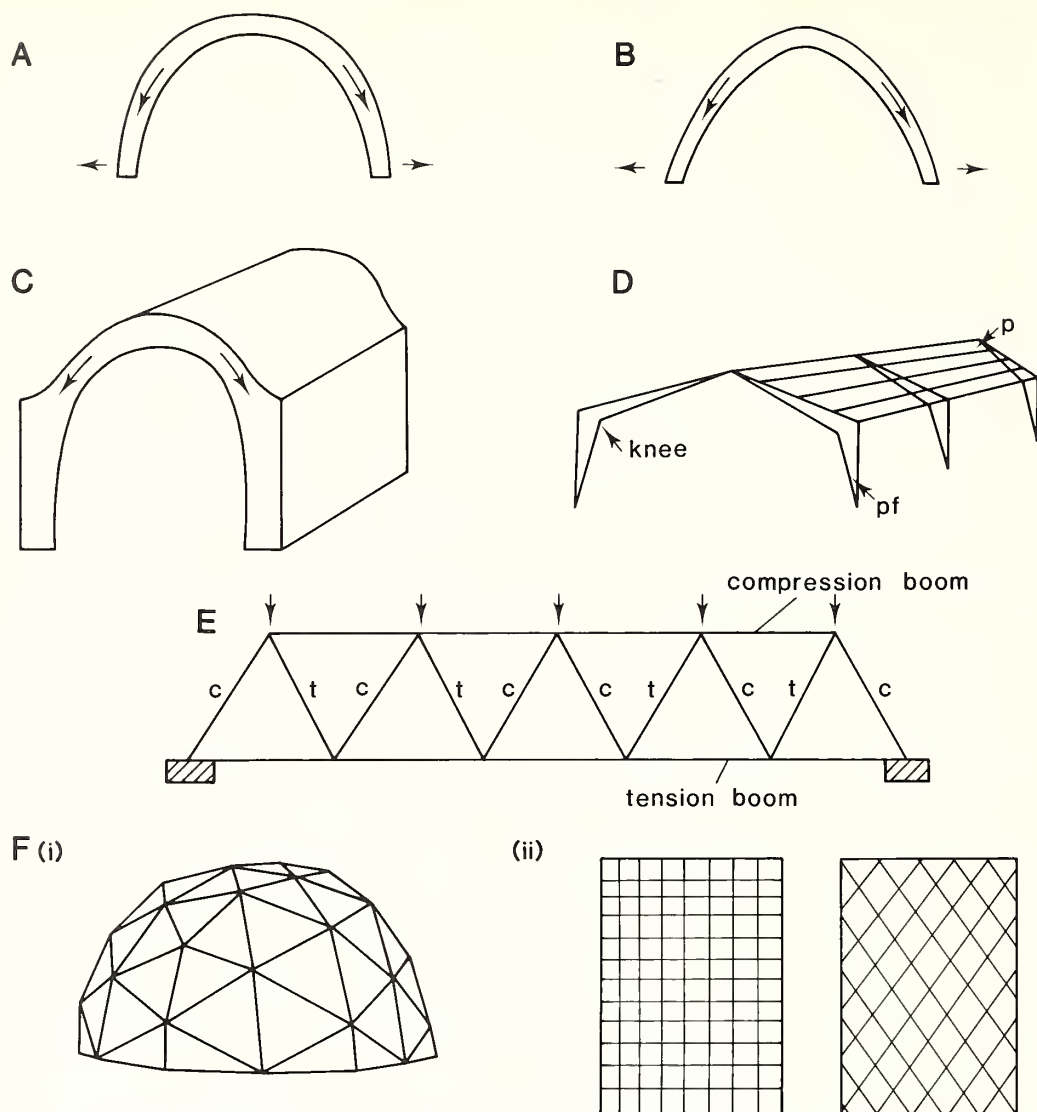
It can therefore be seen that the type of microstructure used to construct a skeleton will influence its mechanical characteristics. Mollusc microstructural types (described by Watabe 1984) have been found to exhibit different mechanical properties despite all being constructed from calcium carbonate. For example, nacre is the strongest, and crossed lamellar structure the hardest. However, mechanical strength may not be the most important factor involved in the design of a skeleton. Although nacre is the strongest of all types of molluscan microstructure and occurred first in the fossil record, weaker structural units are more commonly used today (Currey and Taylor 1974). There is a general correspondence between molluscan microstructure and mode of life (Taylor and Layman 1972; Currey and Taylor 1974; Currey 1976; Gabriel 1981). The development of other shell types may have been due to a necessity to protect against abrasion or chemical attack prevalent in some habitats, at which nacre is relatively poor (Gabriel 1981). The metabolic cost involved in secreting the material may also be more important than its overall strength (Currey 1980). It has been demonstrated that microstructures with a relatively high organic content are more 'expensive' to generate (Palmer 1983). A metabolically cheaper type of microstructure to construct, although of inferior quality to nacre, may be adequate for a particular lifestyle. Oyster shells, for example, are constructed from relatively weak microstructures (foliated structure and chalky deposits) and are prone to attacks from boring organisms; however, they can grow very quickly, which suits these animals' particular mode of life (Currey 1980).

ARCHITECTURE

The general shape of a structure will also influence the way in which it responds to stresses. Structural mechanics have only been applied in any depth to the design of ostracode carapaces, where exoskeletal features have been discussed in relation to common engineering or architectural structures (Benson 1974, 1975, 1981, 1982). Impact and compression testing of ostracode carapaces (Whatley *et al.* 1982) did not reveal any one factor that had overriding importance in conferring strength, though it has been demonstrated that the architecture of cirripede exoskeletons is more important than microstructure (Murdock and Currey 1978).

The importance of shape to the overall mechanical strength of a structure is best explained with reference to common architectural structures. The concept of 'strength through form' (Nervi 1951) has been successfully exploited in architecture from the 1950s. The various man-made constructional forms which have been developed follow well-understood engineering principles, and have many analogies with biological designs. (For an introduction to structural mechanics see Buckle (1977) and Cowan (1980).) Although buildings are many times larger in scale than biological constructions, the forces acting on skeletons generate stresses acting in similar directions.

The type of material to be used usually determines the type of structure that is produced. Due to their different mechanical properties, materials lend themselves to be used in certain ways: for example, stone is relatively weak in tension but possesses great compressive strength.



TEXT-FIG. 2. Space-spanning structures, A, hemisphere. B, dome. C, stone vault; thick walls counteract outward thrusts from the arch and ensure that the forces are deflected to the ground within the structural form (or else the building would collapse). D, portal frames (pf) and purlins (p); portal frames always have a shallow pitch, and the knee is strengthened by increased thickness or reinforcement; the weight and outward thrusts are absorbed by the foundations. E, truss: the girders of the truss act either in tension (T) or compression (C) to take up the load, and have flexible joints (based on Buckle 1977, fig. 8.1). F, space frames: (i), geodesic dome, based on triangular or diamond-shaped grids with flexible joints (from Buckle 1977, fig. 15.3); (ii), lamellar roofs of various shapes are based on horizontal or diagonal grids with rigid joints.

Some of the more common three-dimensional architectural structures are illustrated in Text-figure 2. A catenary is the shape a cable takes when suspended equally at both ends, and can be expressed mathematically as:

$$y = a/2 (e^x + e^{-x})$$

where x and y are coordinates, e = exponential constant, a = variable. When inverted, this form is a catenary arch, on which vertical loads are directed evenly over the whole length. Its three-dimensional extension is the catenary dome (Text-fig. 2B). Although a hemisphere (Text-fig. 2A) encloses a given volume with less surface area than a catenary-shaped dome, the dome is structurally superior at resisting forces directed horizontally, and normally, to the crown. In both structures, the weight of the material is directed downwards, generating horizontal thrusts at the margins. These have to be counteracted either by ring beams, or some other sort of reinforcement such as increased thickness, which confines outward movement of the base.

A vault is another three-dimensional version of an arch, and also has outward thrusts at its base. For stone vaults (Text-fig. 2C), thick adjoining walls are necessary to counteract these horizontal moments and ensure that the thrusts are directed to the foundations within the building structure. This buttressing is essential to prevent collapse. Portal frames are space-spanning structures composed of straight members (Text-fig. 2D). The greatest shear and bending moments occur at the joint between the beam and the column, so the 'knee' is usually strengthened, either by thickening or adding reinforcing material. As with arches, shallower frames are subject to greater horizontal thrusts, and ties can be introduced between the supports to attain equilibrium. Purlins are beams that span between portal frames, and on which additional material can be placed such as roofing tiles. The load acts on the joints between the purlins and the portal frames.

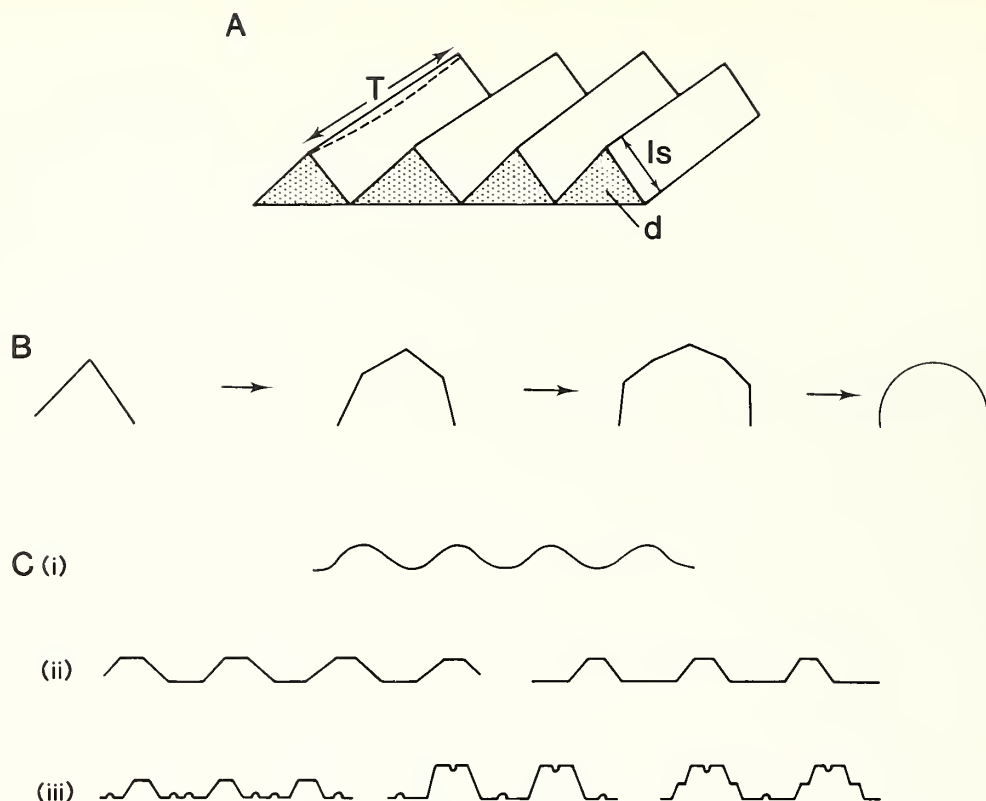
Folded plates and corrugated sheets (Text-fig. 3) are more economical in material than flat plates spanning the same area, as their shape imparts strength and so they can be thinner. A vertical load acting on corrugations is divided into two components: a force R acting at right-angles to the slab surface, and a force P acting parallel to it. P forces are resisted by 'skin stresses' within the slab, so only force R will cause bending. Consequently, much greater forces can be withstood than by a horizontal slab of the same thickness, on which all the force is directed perpendicularly to the surface. A corrugated sheet can withstand up to a hundred times its own weight in load (Cowan 1980): its strength is a function of its sinusoidal cross-section and its overall depth.

As a method of spanning space, a truss (Text-fig. 2E) is more economical in material than a solid beam, and there are many different types. Simply, the stresses from a vertically acting load are taken up by a series of members which act either in tension or compression. Space frames (Text-fig. 2F) can be likened to three-dimensional trusses. Various shaped, strong but lightweight lattices provide the necessary support for thin coverings. As in trusses, the members of the grid act either in tension or compression to transmit the stresses acting on the structure. The covering 'membrane' or 'skin' lies passively between the struts. An alternative type of space frame is the monocoque shell (Benson 1974, 1975), which does not have an internal grid. It is composed of the same material throughout to produce a strong thin shell, and all the load is transmitted through this thin 'stressed skin'.

INFLUENCES OF TRILOBITE CUTICLE COMPOSITION AND MICROSTRUCTURE ON MECHANICAL BEHAVIOUR

Since the organic matrix has so much influence on the mechanical behaviour of heavily mineralized exoskeletons, no mechanical tests were performed in this study on fossil material, as any remaining organic matter will have been degraded. This has been proved for ostracodes by compression and impact tests on fossil and Recent specimens of the same species (Whatley *et al.* 1982), which were found to have different strengths. However, knowledge of trilobite microstructure (Wilmot 1988) can still provide much information on the likely mechanical properties of the exoskeleton.

Trilobite exoskeletons were heavily calcified, composed predominantly of low-magnesian calcite (Wilmot and Fallick 1989) with only a small proportion of organic matter. In this respect they can be categorized with other stony skeletons as behaving as ceramics. Remnants of the organic matrix have been obtained by decalcifying the cuticles in EDTA (Dalingwater 1969, 1973; Teigler and Towe 1975; Miller 1976; Dalingwater and Miller 1977). Although the composition remains uncertain, it may well have consisted of proteins and chitin fibrils as in all other arthropods.



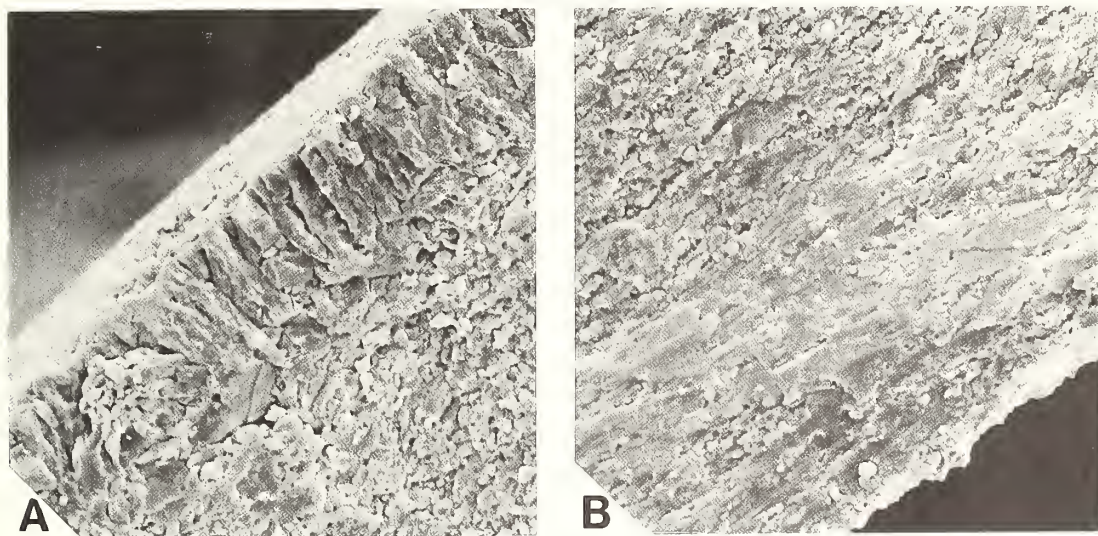
TEXT-FIG. 3. Corrugations. A, folded sheet: there is only a small local span (ls) so only thin slabs are necessary to resist the R and P forces; thin, end diaphragms (d) resist the thrusts (T) from the whole roof (based on Buckle 1977, fig. 14.7). B, the more folds in the folded sheet, the less local bending, enabling thinner slabs to be used, therefore sinusoidal corrugations are the strongest. C, examples of various profiles of corrugations used in buildings: (i), sinusoidal; (ii), trapezoidal (symmetrical and asymmetrical); (iii), stiffened trapezoidal.

Like all exoskeletons, trilobite cuticles were used both for protecting and supporting the viscera, and would have been subject to both tensile and compressive forces. Tensile forces parallel to the surface would have been present within the domed structure of the skeleton, and to a lesser extent generated by the suspension of the viscera. Compressive stresses would have been imposed by water currents and predators. To resist these, the exoskeleton contained tension elements, probably long chitin fibrils orientated parallel to the cuticle surface, and short calcite crystals strong under compression.

Unmineralized insect cuticle is stronger and stiffer than calcified crustacean cuticle; crustacean exoskeletons have to be thicker to compensate (Wainwright *et al.* 1976). However, calcification is very common in the marine environment as calcium ions are readily available. Hence it is much more economical for a marine invertebrate to construct an exoskeleton consisting of less protein and more calcium carbonate in comparison with its terrestrial counterpart (Wainwright *et al.* 1976). This probably explains why trilobite exoskeletons were heavily calcified.

Apart from agnostid exoskeletons which may have been constructed of only a thin, prismatic layer (Wilmot 1990a), most calcified trilobite cuticles comprise an outer prismatic layer with a thicker principal layer below. Sometimes the thin outer layer is finely laminated (Mutvei 1981; J. E. Dalingswater pers. comm.). Prismatic layer is a relatively thin layer of calcite crystals, approximately $1\text{ }\mu\text{m}$ in diameter, orientated with their longer c -axes perpendicular to the outer

surface (Text-fig. 4A). It is not analogous to the molluscan prismatic layer which can have crystals up to several millimetres long, with each surrounded by a thick ($5\text{ }\mu\text{m}$) layer of organic matrix (Currey 1980). Trilobite principal layer forms 85–95% of the total cuticle thickness. It is finer grained, and has a much less regular crystal arrangement than the prismatic layer (Text-fig. 4B). Parallel laminations are sometimes preserved within this layer which may mark the former positions of organic material. The amount of organic matrix was low, with much less than $1\text{ }\mu\text{m}$ thickness between crystals. As in molluscan nacre (Currey 1980), fracture of trilobite exoskeletons mainly occurred through the thin layers of organic matter rather than through individual calcite crystals (unpublished observation, see Text-fig. 4). Except for eye lenses which were necessarily always of extremely high quality calcite, none of the cuticular crystals have two axes more than $3\text{ }\mu\text{m}$ long, so minimizing the risk of dangerously large internal defects.



TEXT-FIG. 4. Scanning electron micrographs of trilobite cuticular structure, exposed on a vertical fracture surface. *Phacops rana crassituberculata* Stumm, NMW.88.22G.41, Silica Shale, Silica, Ohio (Middle Devonian), $\times 1500$. A, prismatic layer with calcite crystals ($1 \times 10\text{ }\mu\text{m}$) orientated with their c-axes perpendicular to the surface; note that fracture has occurred between crystals, not through them. B, principal layer, with calcite crystals aligned parallel to the surface.

It has been argued above that the type of microstructure used is a compromise between the mechanical properties necessary for a particular mode of life, and the metabolic price that has to be paid in order to construct it. Trilobites, like other arthropods, regularly had to shed their exoskeletons in order to grow. Immediately after moulting, the organism would have been unable to move or feed properly, as well as being very vulnerable to predation, and so it would have been advantageous to mineralize the cuticle as soon as possible. It is therefore likely that rapidity of calcification was one of the main priorities involved in the selection of microstructure. Modern mollusc shells are stronger than crustacean cuticles (Wainwright *et al.* 1976), but such shells are gradually secreted throughout life. When trilobite cuticle was secreted, the prismatic layer formed first, with only a very thin principal layer present; as secretion continued, cuticle thickness increased by addition to the principal layer (Miller and Clarkson 1980). This suggests that the prismatic layer was relatively easy to generate, being calcified rapidly after ecdysis to give some degree of hardening to the cuticle. Bulk was added later to the exoskeleton to give greater strength. Prismatic layer may also have been effective against shell-boring organisms, as with molluscs (Gabriel 1981). Trilobite prismatic layer with its regular crystal arrangement was probably quite strong under compressive forces acting normal to the cuticle surface, but would have had poor crack-stopping capabilities. A

crack would have been able to travel unimpeded between crystals, and would only have been deflected on reaching the principal layer: hence the need for a thin principal layer even in newly secreted cuticle. The crack-stopping abilities of the principal layer can still be effective after millions of years: prismatic layer is often lost from trilobite cuticles when they are extracted from the rock matrix, whereas the principal layer remains intact (Miller 1976).

Unlike molluscs, trilobites only developed two kinds of exoskeletal microstructure. However, the overall thickness of the cuticles and the relative proportions of the different layers do vary considerably, which would have been of mechanical significance. Different types of cuticular ultrastructure may have been related to mode of life, or may just have been a phylogenetic trait, e.g. proetides have relatively thin prismatic layers.

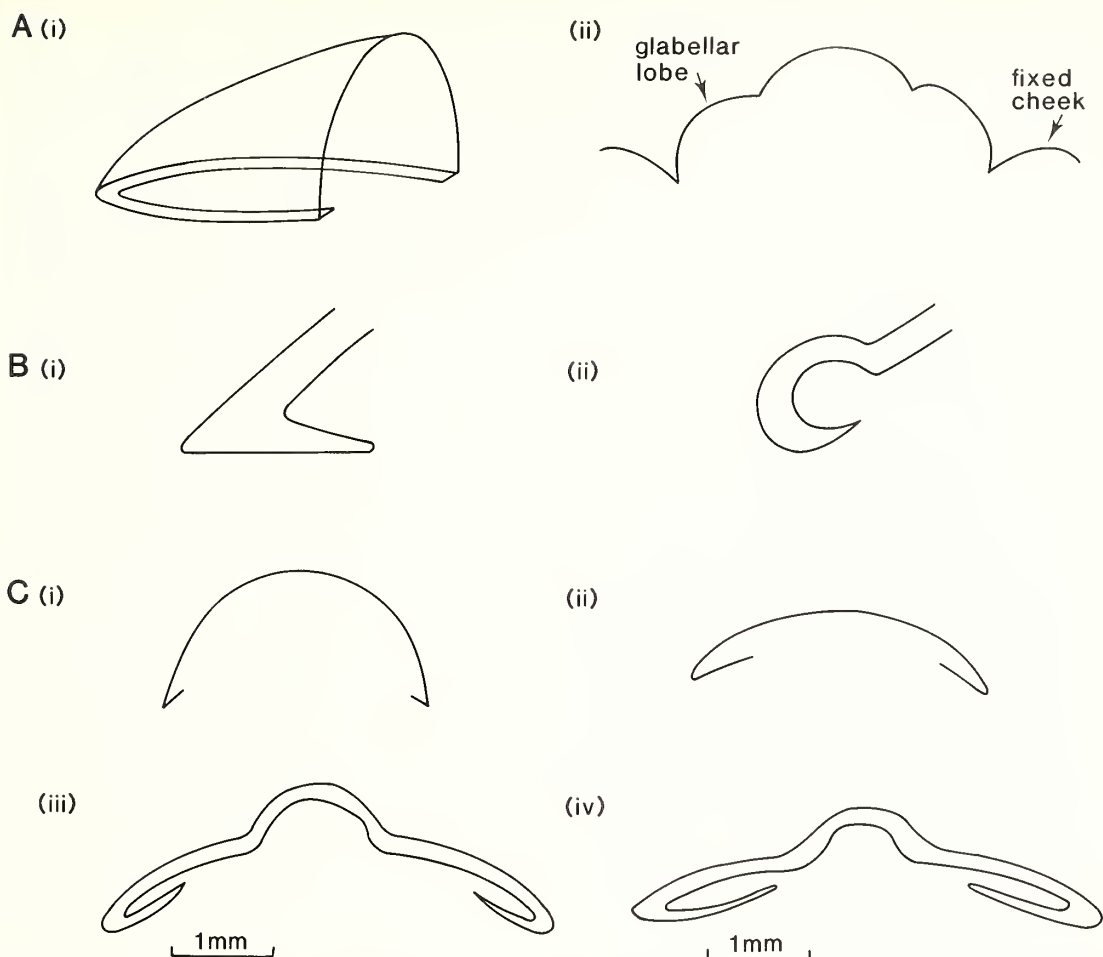
EFFECTS OF TRILOBITE ARCHITECTURAL DESIGN ON MECHANICAL STRENGTH

When assessing the design of an exoskeleton, it is important to consider the main function it provides for the animal. In trilobites, it seems likely that the exoskeleton developed primarily as a means of protection against predators, rather than just for muscle support. The high degree of calcification of the cuticle compared with other arthropods suggests an evolutionary bias for thicker exoskeletons and hence increased protection. Indeed, in low-oxygenated environments such as those existing in the 'Olenid Sea', predation was rare and the predominant trilobites only had very thin cuticles (Fortey 1985).

Other evidence suggesting a defensive function for the cuticle is the development of sophisticated enrolment mechanisms. This was a great advantage to trilobites, as they were able to curl up into 'balls' that enclosed vulnerable soft parts within the calcified exoskeleton. The cuticle then effectively formed a hard, protective outer casing with a much greater diameter than before, and the animal was therefore more difficult to attack. As cuticle thickness was fairly uniform throughout (increasing at muscle insertion areas), there were no major weak points in the 'ball' that could be exploited by predators. The margins of the exoskeleton, such as the borders of the cephalon and pygidium were often locked tightly together and, due to the doublure, were also thicker and stronger regions. Pleurae overlapping articulating facets greatly increased 'ball' thickness laterally. Detailed methods of trilobite articulation and enrolment are well known and will not be discussed further here: see Harrington (1959, pp. O70–O73, figs 49–51), Bergström (1973), and Fortey and Owens (1979) for further information.

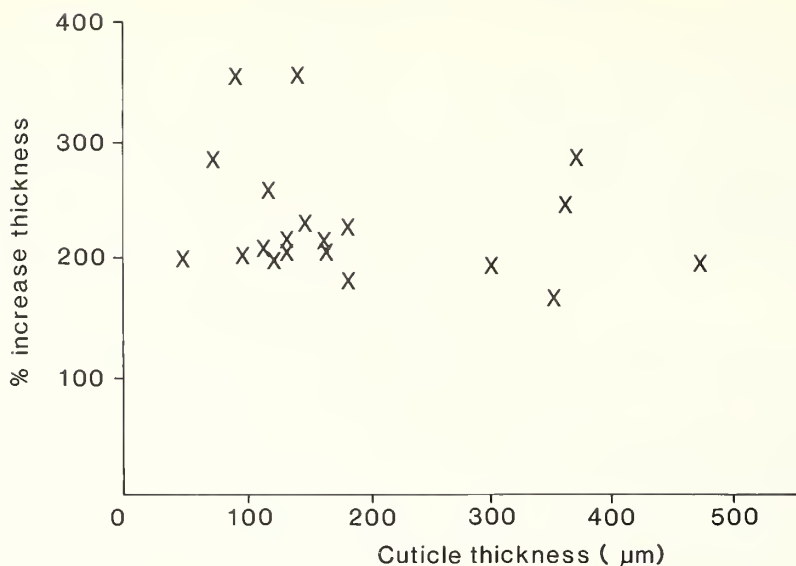
Although it can be seen that the trilobite exoskeleton was well developed for enrolment, the general shape was also mechanically strong for 'normal' life situations, and it is this aspect which will be discussed further below. For example, although the doublure may sometimes be involved in enrolment, incorporating coaptative devices (Clarkson and Henry 1973), this alone cannot explain its function for all trilobites. Schmalfuss (1981) suggested that doublures with terrace ridges supported a respiratory and feeding chamber below the animal, but this is unlikely to be true of pelagic species, or groups with long pygidial doublures (Fortey 1985). It is proposed here that the doublure acted primarily as a structural strengthening device, necessary for a dome-shaped exoskeleton.

Like most ostracode carapaces, the trilobite exoskeleton structurally most resembles a series of modified domes based on catenary arches (Text-fig. 5). The cephalon and pygidium can be regarded simply as half-domes. The horizontal thrusts at the margins of the domes are resisted by the doublure, which confers strength by increased thickness and a change of direction. The inner edge of the doublure marks the point of attachment of the ventral membrane, but although the latter was probably tough, its flexibility (Müller and Walossek 1987) would have given it negligible structural strengthening properties. Its main function would have been to constrain the positions of the body organs. As with the knee of a portal frame constructed of the same material throughout, the exoskeleton also had to be thicker at the doublure to resist shear forces acting at the change of direction. On average, cuticle thickness at least doubles at the doublure (Text-fig. 6). As slightly



TEXT-FIG. 5. General form of cephalon and pygidia. A (i), trilobite cephalon and pygidia can be regarded simply as half-domes; A (ii), generalized transverse section through a cranidium; the basic shape of a half-dome has been modified by addition of extra domes. B (i), the doublure gives strength to the domed structure by increasing thickness at the base, and a change of direction; B (ii), the shape of the doublure is also important; cylindrical doublures such as those of certain proetids are very strong. C, flatter domes exert greater thrusts at the margins and therefore need longer doublures: (i), (ii), diagrammatic representation of the relationship between convexity and doublure length; (iii), transverse section through the pygidium of *Proetus* (*Proetus*) *concinus* (Dalman) (based on specimen NMW.88.22G.42); (iv), transverse section through the pygidium of *Warburgella* (*Warburgella*) *stokesii* (Murchison) (based on specimen NMW.88.22G.43); both these trilobites belong to the Proetacea yet have slightly different convexities, and hence dissimilar doublure lengths.

oblique sections through the doublure would give the impression of increased cuticle thickness, the minimum values recorded are the most significant. The width of the doublure is proportional to its strength (longer doublures affording more resistance to thrusts), therefore flatter domes which exert greater horizontal thrusts have to have longer doublures (Text-fig. 5c). However this general relationship is not necessarily valid for all trilobites, as factors such as doublure shape, ultrastructure, and overall cuticle thickness also exert an effect. Different types of trilobite doublure are illustrated in Text-figure 7. The addition of extra domes to parts of the exoskeleton such as the glabella (Text-fig. 5A (ii)) is also a recognized practice in architecture.



TEXT-FIG. 6. Increase in cuticle thickness across the doublure.

Although, in sagittal section, a trilobite is much more elongated and therefore resembles a shallower dome than in transverse section, the thorax is well jointed, and dorso-ventral forces could have been taken up by flexure (Text-fig. 7A (iv)). However, the main purpose of the jointed thorax was for locomotion and enrolment.

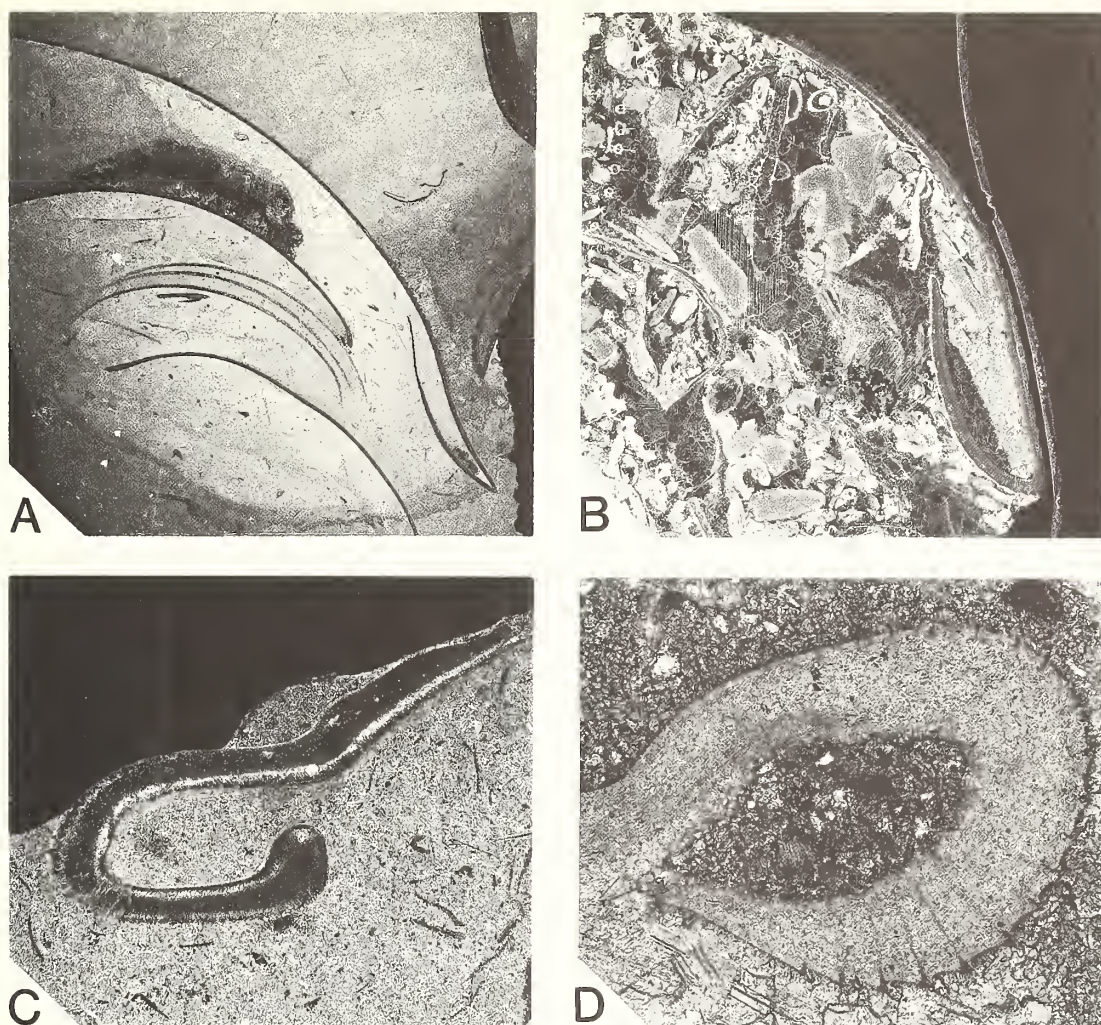
Trilobite thoracic segments are a compromise in structure between the necessary mechanical strength to protect and support the underlying organs, and permitting articulation. Some trilobites, such as certain illaenimorphs and homalonotids are characterized by their high convexity and effacement. Their thoracic segments resemble single arches (Text-fig. 8B) and are therefore structurally strong, and articulate only at the two fulcra (Lane and Thomas *in* Thomas 1978; Thomas and Lane 1984). The segments are arranged in an imbricate manner, and articulation is achieved by them sliding underneath one another (Thomas and Lane 1984, Text-fig. 2D). However, this is not common for trilobites as a whole.

Most trilobites have various structures on the anterior and posterior margins of the thoracic segments which enable them to articulate. These may include an articulating half-ring anterior to the axial ring, flanges from the proximal parts of the pleurae to the fulcra, fulcral processes with corresponding sockets, and articulating facets on the distal parts of the pleurae (Harrington 1959). Additionally, coaptative structures may exist on the cephalon and pygidium (Clarkson and Henry 1973; Henry and Clarkson 1975).

Many thoracic segments have the proximal parts of the pleurae extending horizontally from the axial furrows (Text-fig. 9). Although this is not very strong structurally, it is of great importance in articulation as the pleurae form a hinge plane. Strengthening of these thoracic segments is generated by the axial and pleural furrows (Bergström 1973; Müller and Walossek 1987) which are expressed ventrally as ridges (Text-fig. 9G), thus turning the cuticle into a folded sheet. Additional thickening of the exoskeleton in these areas also increases the strength of the structure, especially in areas of muscle attachment such as the axial furrows.

Other thoracic segments are intermediate in form between these two end members and resemble arches on arches, but with several articulating processes (Text-fig. 10). Therefore, although the cephalon and pygidium of a trilobite are well designed for mechanical strength, the shape of thoracic segments are also a function of their role in articulation.

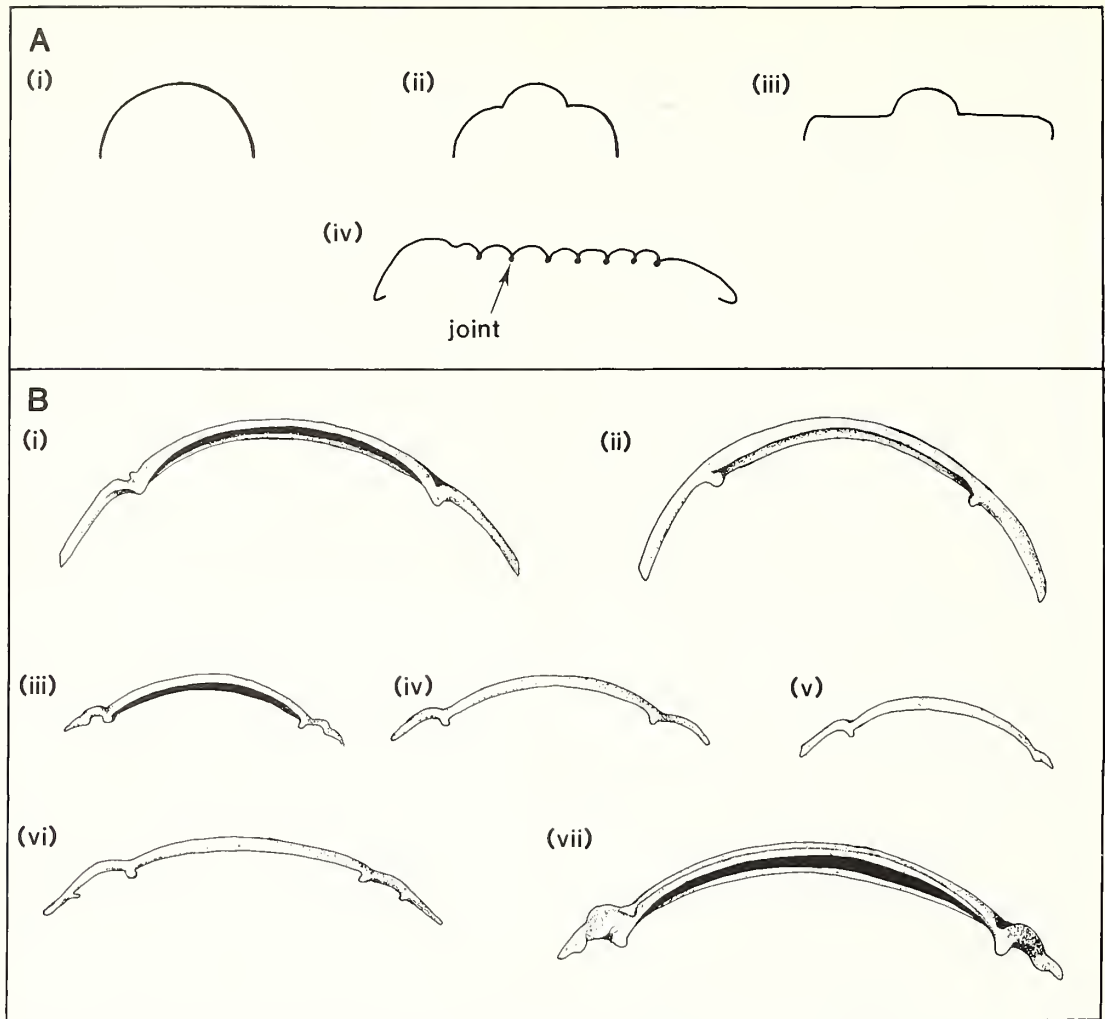
Occasionally a network of polygonal structures can be seen on the surface of trilobite cuticles, for



TEXT-FIG. 7. Different types of doublure. A, *Illaeus* sp. (JED) 2 Feb. 1966, pygidial doublure, Boda Limestone, Dalarna, Öland (Ordovician), $\times 15$. B, *Cybantyx anaglyptos* Lane and Thomas, NMW.88.22G.21, longitudinal section through pygidium. Much Wenlock Limestone Formation, Wren's Nest, Dudley (Wenlock), $\times 7$. C, *Dalmanites myops* (König), NMW.88.22G.20, longitudinal section through pygidium, Hill End Farm Borehole, Walsall (Wenlock), $\times 10$. D, *Warburgella (Warburgella) stokesii* (Murchison), NMW.88.22G.5, transverse section through the lateral border of a free cheek (note the canals opening out at the crests of the terrace ridges), Coalbrookdale formation, Daw End railway cutting, Walsall (Wenlock), $\times 70$.

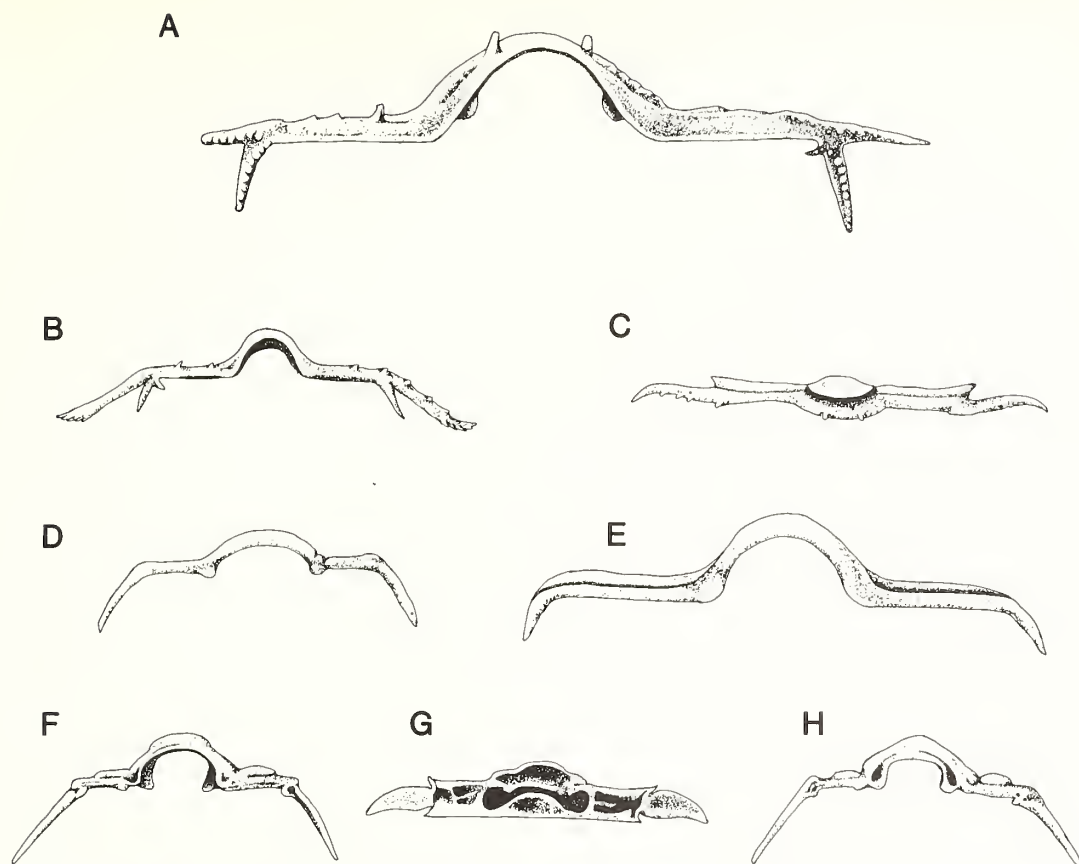
example *Homagnostus obesus* (Wilmot 1990a) which gives the appearance of space frames, such as geodesic domes. However, as trilobite exoskeletons were constructed predominantly from low-magnesian calcite, their space-enclosing structure is more analogous to the monocoque shell, which resists forces throughout its 'skin', not just in members of a grid system.

The polygonal structures may simply be the external expression of epidermal cells which generated the cuticle (Wilmot 1990b), but the network of ridges they create can give the 'thin shell' some additional strength. When examined in detail, the cell polygons are essentially curved plates with reinforced ridges on their edges (Text-fig. 11A, B). In section, the ridges are acting as T-beams



TEXT-FIG. 8. Trilobite thoracic segments. A, generalized forms of trilobite thoracic segments: (i), single arch; (ii), arch on arches; (iii), horizontal pleurae; (iv), simplified sagittal section through a trilobite, emphasizing the relatively low convexity compared with transverse sections, and the jointed nature of the thorax. B, single arch thoracic segments: (i), (ii), *Bumastus (Bumastoides) lenzi* Chatterton and Ludvigsen (Illaenidae), anterior and posterior views of thoracic segments, $\times 3.8$ (based on Chatterton and Ludvigsen 1976, pl. 5, figs 27 and 31). (iii)–(vii), *Failleana calva* Chatterton and Ludvigsen (Styginidae), thoracic segments (based on Chatterton and Ludvigsen 1976, pl. 6): (iii), anterior view, $\times 3$ (fig. 18); (iv), posterior view, $\times 4.3$ (fig. 21); (v), posterior view, $\times 2.9$ (fig. 24); (vi), posterior view, $\times 4.3$ (fig. 22); (vii), anterior view, $\times 3.5$ (fig. 27).

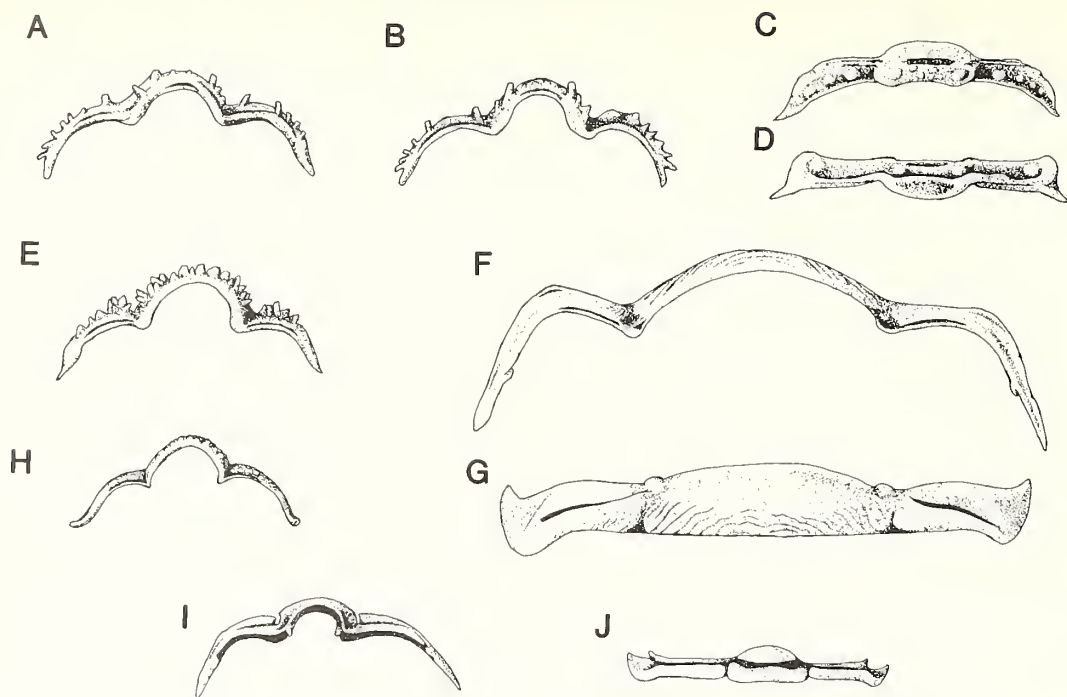
(Text-fig. 11c), which are much stronger than ordinary beams with columns since there are no joints. Although in architecture these are normally inverted, the principles involved remain valid for trilobites. Altogether, a strengthening meshwork has been produced over the external surface, the structural significance of which is most marked in thin cuticles such as those of agnostid trilobites, where the ridges can form as much as 15% of the total cuticle thickness. Such grids are rarely used in man-made structures as external meshes are subject to corrosion; as a compromise, they have to be placed within the structure. In this respect therefore, trilobite exoskeletons are better designed than most buildings, although an external mesh was applied to the Philips Pavilion, designed by Le



TEXT-FIG. 9. Thoracic segments with horizontal pleurac. A, *Ceratocephala lacinata* Whittington and Evitt (Odontopleuridae), posterior view of thoracic segment, $\times 10$ (based on Whittington and Evitt 1954, pl. 8, fig. 8). B, C, *Acidaspis (Acidaspis) lespancei* Chatterton and Perry (Odontopleuridae), posterior and anterior views of thoracic segment, $\times 10$ (based on Chatterton and Perry 1983, pl. 21, figs 15 and 16). D, *Nanillaenus mackenziensis* Chatterton and Ludvigsen (Illaenidae), anterior view of thoracic segment, $\times 2.9$ (based on Chatterton and Ludvigsen 1976, pl. 4, fig. 15). E, *Dolichoharpes* aff. *D. reticulata* Whittington (Harpedidae), posterior view of thoracic segment, $\times 7$ (based on Chatterton and Ludvigsen 1976, pl. 7, fig. 24). F-H, *Ceraurinella typa* Cooper (Cheiruridae), anterior, ventral and posterior views of thoracic segment, $\times 2$ (based on Whittington and Evitt 1954, pl. 11, figs 1, 4, 5).

Corbusier at the Brussels Exhibition in 1958. As the building was a temporary exhibit, corrosional effects were unimportant.

Additional structures on trilobite exoskeletons acting as T-beams occur on the ventral surfaces of some effaced cuticles (Text-fig. 11E). For example, the pygidium of *Leiolichas* is strengthened by a series of radiating ribs (Thomas and Holloway 1988, pl. 9, fig. 208). As mentioned previously, ridges on the ventral surface are generally more prominent than the corresponding dorsal furrows, although this is probably primarily for muscle attachment rather than for strengthening purposes. Other larger-scale features such as terrace ridges will have strengthened the exoskeleton by increasing the thickness of the cuticle. As most terrace ridges only have relief on the external surface of the exoskeleton, they acted mechanically as reinforcing ridges to the 'sheet', and often occur on the margins or doublure where strains were greatest. Those that have relief on both dorsal and ventral surfaces of the cuticle (Wilmot 1988) will have acted as folded plates.



TEXT-FIG. 10. Arch-on-arch thoracic segments. A-D, *Dimeropyge virginensis* Whittington and Evitt (Dimeropygidae), thoracic segments, $\times 15$ (based on Whittington and Evitt 1954, pl. 3, figs 8, 11, 1, 5). E, *Dimeropyge clintonensis* Shaw (Dimeropygidae), posterior view of thoracic segment, $\times 15$ (based on Chatterton and Ludvigsen 1976, pl. 18, fig. 11). F, G, *Isotelus parvirugosus* Chatterton and Ludvigsen (Asaphidae), posterior and dorsal views of thoracic segment, $\times 2.9$ (based on Chatterton and Ludvigsen 1976, pl. 2, figs 19 and 20). H, *Acanthoparypha chiropyga* Whittington and Evitt (Cheiruridae), posterior view of thoracic segment, $\times 3.2$ (based on Whittington and Evitt 1954, pl. 29, fig. 25). I, J, *Encrinuroides rarus* (Walcott) (Encrinuridae), posterior and dorsal views of thoracic segments, $\times 5.5$ (based on Chatterton and Ludvigsen 1976, pl. 15, figs 40 and 41).

CONCLUSIONS

1. For the first time, the mechanical characteristics of a trilobite exoskeleton have been related to its composition, microstructure, and architecture.

2. Trilobite cuticles are best regarded as ceramics which are linearly elastic, as they were predominantly composed of low-magnesian calcite with only a small proportion of organic matter.

3. Calcification was probably the most economical method of strengthening the cuticle in the marine environment, due to the abundance of the relevant ions.

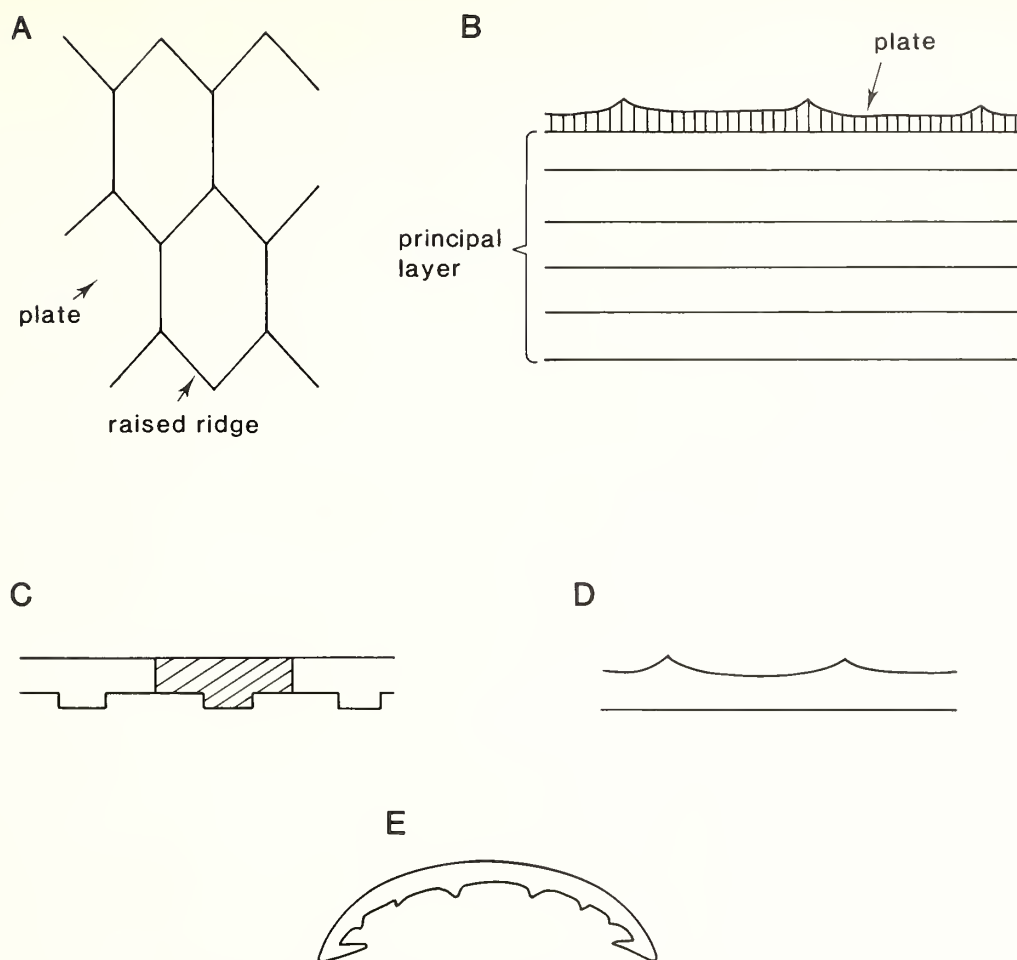
4. Trilobite exoskeletons were composites that could resist both tensile and compressive forces.

5. The small size of the calcite crystals reduced the risk of crack formation, and the progression of fractures was slowed by the changes of direction at each crystal boundary.

6. Prismatic layer was probably the easiest microstructure to generate, being rapidly calcified after ecdysis, and would have been strong under compressive forces acting normal to the cuticle surface. The underlying principal layer functioned as a crack-stopper and added bulk to the exoskeleton.

7. The relative proportions of prismatic layer to principal layer would have been of mechanical significance.

8. Structurally, the trilobite exoskeleton is a monocoque shell in the form of a series of modified



TEXT-FIG. 11. T-beams. A, plan view of cell polygons on trilobite cuticle. B, schematic transverse section through trilobite cuticle, not to scale. C, T-beam, as used in architecture. D, transverse section through an agnostid cuticle. E, schematic transverse section through an effaced pygidium showing ribs on ventral surface.

domes. The doublure, cell polygons, and terrace ridges all strengthened the cuticle. Strongly convex trilobites had shorter doublures than shallower forms.

9. The shape of thoracic segments is a compromise between mechanical strength and their function as articulating structures.

Acknowledgements. This work was carried out as part of a Ph.D. thesis funded by an Aston University Research Studentship Award. I thank Dr A. T. Thomas for his encouragement and supervision throughout the project, and my father for valuable discussions on structural mechanics and architectural design. The manuscript has also benefited from the comments of Professor J. D. Currey. All material is housed at the National Museum of Wales, Cardiff, accession number NMW 88.22G, or as part of the collections of Dr J. E. Dalingwater (JED), University of Manchester, also housed in Cardiff.

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Typescript received 15 May 1989

Revised typescript received 15 February 1990

THE SILURIAN RUGOSE CORAL GENUS *ENTELOPHYLLUM* AND RELATED GENERA IN NORTHERN EUROPE

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ABSTRACT. Restudy of *Entelophyllum* from Gotland (including the type species) and Great Britain indicates restriction of *Entelophyllum* to phaceloid forms with peripheral, parricidal increase. Typical forms also have smooth or carinate septa, well-developed biserial tabularia, and dissepimentaria composed of globose interseptal dissepiments. On Gotland the genus ranges from the late Telychian to the Ludfordian. *Stereoxylodes* Wang and *Carinophyllum* Strelnikov are considered junior synonyms of *Entelophyllum*. Species from Gotland with nonparricidal budding are referred to *Donacophyllum* Dybowski. Cerioid forms internally similar to *Entelophyllum* are referred to *Prohexagonaria* Merriam. *Petrozium* Smith is retained for some Early Silurian forms. Newly described taxa are: *Entelophyllum articulatum anglicum* subsp. nov., *E. dendroides* sp. nov., *E. lauense* sp. nov., *E. hamraense* sp. nov., *E. sp. A*, *Prohexagonaria favia* sp. nov., *P. gotlandica* sp. nov., *Donacophyllum neumani* sp. nov., and *D. wallstenense* sp. nov.

ENTELOPHYLLUM was proposed by Wedekind in September 1927, and Lang and Smith described *Xylodes* in October of the same year, both for Silurian rugose corals similar to *Cyathophyllum articulatum* Wahlenberg, 1821. Since 1927, many forms worldwide have been referred to *Entelophyllum* and other genera have been based on species referred to it at one time or another. Several of the early species were based on unsectioned specimens, some of which have since been lost or destroyed. Variation and stratigraphic distribution of most species were unknown. Consequently, many of the species have been misinterpreted and some identifications away from the type areas are clearly inaccurate.

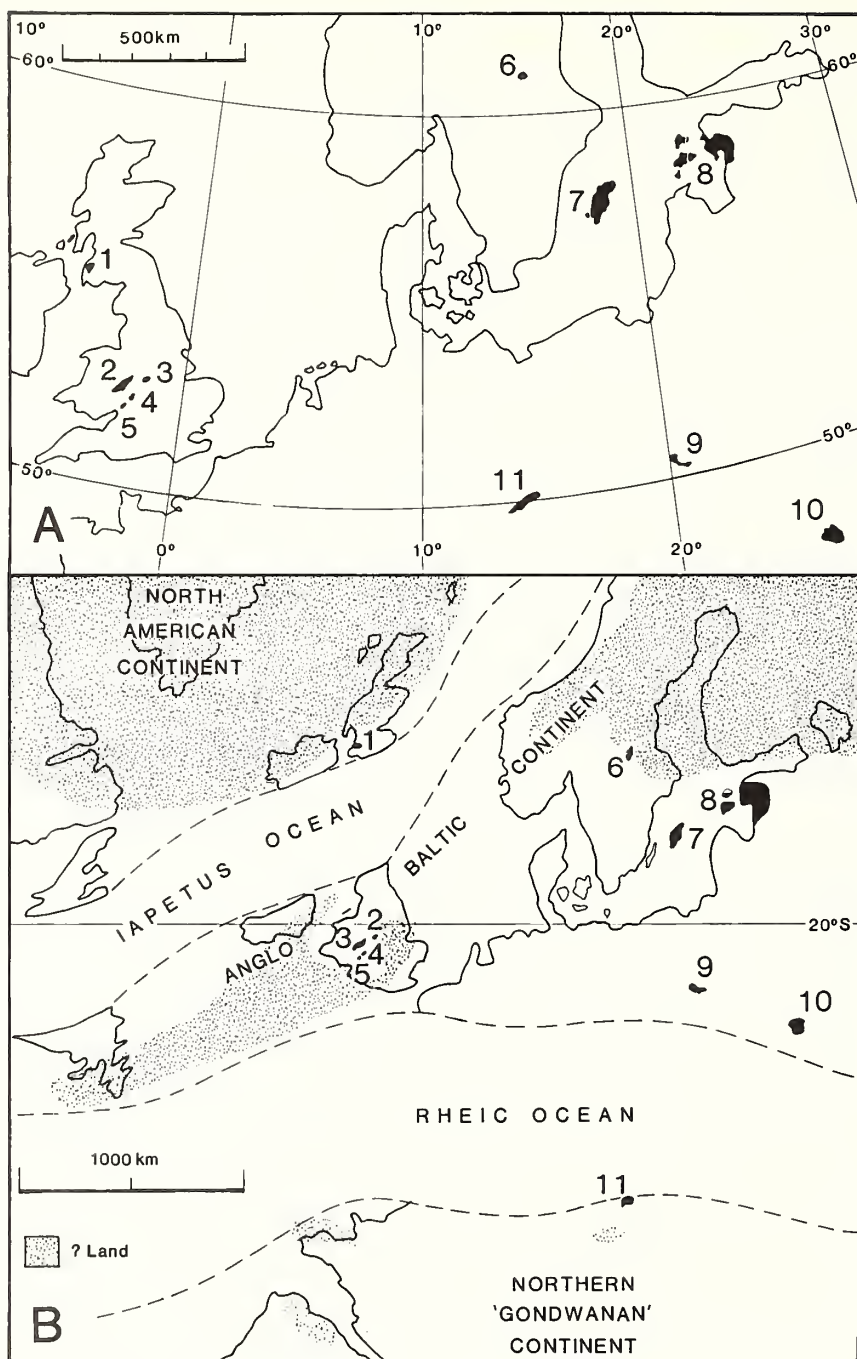
The Silurian sequence on Gotland, Sweden (Text-fig. 1A) is the type area for several species and provides the best succession of entelophylloid corals worldwide. This restudy is based on collections in the Riksmuseet, Stockholm, Dr B. Neuman's collection in Bergen, Professor D. Hill's collection in the University of Queensland, and on large collections made by the authors in 1972. We have studied the available English and Scottish material in the collections of various British museums and have collected from many of the British sections. Our descriptions and interpretations of other northwestern European occurrences of entelophylloid corals are based on the published data and photographs of type material sent to us by various colleagues. It is hoped that this study will provide a significant basis for the re-evaluation of such corals from other regions in the world.

STRATIGRAPHY AND DISTRIBUTION

Great Britain

The earliest known occurrence of entelophylloid corals in Britain is *Petrozium dewari* Smith in the Llandovery (possibly late Rhuddanian: based on correlations by Cocks and Toghiani 1973), of southwestern Scotland. In Shropshire, it occurs in the Pentamerus Beds, the graptolites of which are attributable to the early Telychian *turriculatus* Biozone, and in the overlying Hughley Shale (Ziegler *et al.* 1968) (Text-figs 2 and 3).

Entelophyllum has not been recorded from the Sheinwoodian Stage in Britain as this interval is generally noncalcareous but as the sequence becomes more calcareous, *E. articulatum anglicum*



TEXT-FIG. 1. A, Distribution of entelophylloid corals in northern Europe. B, Palaeogeography for mid-Silurian times based mainly on Cocks and Fortey (1982) and McKerrow (1988). Localities: 1, Girvan; 2, Wenlock Edge; 3, Dudley; 4, Malverns; 5, May Hill; 6, Dalecarlia; 7, Gotland; 8, Estonia; 9, Holy Cross Mountains; 10, Podolia; 11, Bohemia.

subsp. nov. and *E. pseudodianthus* (Weissermel) appear together in the Homerician Much Wenlock Limestone at Dudley, Worcestershire. In Shropshire, specimens from the middle Homerician Farley Member of the Coalbrookdale Formation have been referred to both of the above species. The overlying Much Wenlock Limestone, which along Wenlock Edge is late Homerician (Bassett *et al.* 1975), yields both species. Both *E. articulatum anglicum* and *E. pseudodianthus* are known from the lower Elton Beds of early Gorstian age (Holland *et al.* 1980).

CHRONOSTRATIGRAPHY SERIES		ENGLAND		GOTLAND	ESTONIA	PODOLIA	BOHEMIA	
PRIDOLI		Ledbury	SW NE	Sundre Hamra	Ohesaare	Dzwinogorod	Pridoli	PRIDOLI
		Temeside			Keugutuma	Rashkov		
		Downton Castle						
LUDLOW	LUDFORDIAN	Whitcliffe	Burgsvik Eke	Hemse	Kuresseare	Isakovtsy	Kopanina	LUDF
		Leintwardine				Grinchuk		
	GORSTIAN	Bringewood			Peadla	Sokol		GOR
		Elton				Konovka		
		Much Wenlock						
WENLOCK	HOMERIAN	Farley	Mulde Slite Höglint Visby Röda Lagret	Halla Tofta Upper Lower	Rootsiküla	Ustje	Motol	HOMER
		Coalbrookdale			Jaegarehu	Muksha		
	SHEINWOODIAN	Buildwas			Jeani	Cherch Maryanovka Demshin Restevo		SHEIN
LLANDOVERY	TELYCHIAN	Hughley	Not Exposed	Velise Rumba Raikküla Saarde Tamsalu Verbola			Litohlevy	TELY
	AERONIAN	Pentamerus						
	RHUDDANIAN	Kenley						

TEXT-FIG. 2. Correlation of standard Silurian chronostratigraphic units and the principal entelophylloid bearing sequences of northern Europe; correlations based on Holland and Bassett (1989).

Gotland

Where possible, Gotland collections are related to localities of Laufeld (1974) and to geological mapping of Hede (1960). The earliest occurrence is *Entelophyllum dendroides* sp. nov. (Text-fig. 3) from the Telychian Röda Lagret, which crops out just below sea level north of Visby.

Prohexagonaria favia sp. nov. occurs in the Sheinwoodian Upper Visby Beds. Wedekind (1927) described *E. visbyense* and *E. anschutzi* from early Sheinwoodian Höglint Beds at Visby. Neuman and Hanken (1979) listed *E. visbyense* in the top of the Upper Visby Beds southwest of Visby. We consider these two species synonymous and probably not referable to *Entelophyllum* s.s.

The neotype of *E. articulatum* is from an unknown locality and horizon on Gotland but it is closely similar to specimens occurring in the early Homerician Slite Beds at Bogeclint l. It also occurs in the Homerician Mulde and Klinteberg Beds and its highest occurrence is in the Gorstian lower part of the Hemse Beds at Snoder l.

Entelophyllum proliferum (Dybowski) was described from the island of Stora Karlsö in the upper part of the Slite Group (late Sheinwoodian to early Homerician age). From the northwestern coast of Stora Karlsö we describe *Donacophyllum nemmani* sp. nov. and *D. wallstenense* sp. nov., which are similar to *E. articulatum* except in mode of increase and in development of lonsdaleoid dissepiments.

E. fasciculatum Wedekind, which descended from *E. articulatum*, is common in the upper Hemse and Eke Beds, the shelly faunas of which suggest an early Ludfordian age (Bassett and Cocks 1974). Of heavily carinate forms, *E. lauense* sp. nov. appears in the Eke Beds and *E. hamraense* sp. nov. occurs in the late Ludfordian Hamra and Sundre Beds.

Central Sweden

The only suggestion of *Entelophyllum* from mainland Sweden is one specimen described by Lindström (1880) as *Cyathophyllum dalecarlicum*. No further material has been found and its assignment is questionable. It is from the Telychian (based on graptolites listed by Hede 1958) in central Sweden.

Estonia

Petrozium losseni (Dybowski) from the late Rhuddanian, upper Juuru Horizon is the oldest known entelophylloid from Estonia (Text-fig. 3). Kaljo (1970) listed *E. articulatum* in the Telychian Adavere Horizon, *E. articulatum* and *E. pseudodiantus* in the late Ludfordian Kuressaare Horizon and in the Pridoli Ohesaare Horizon (Text-fig. 2). These forms are almost certainly not conspecific with English and Gotland species. Fedorowski and Gorianov (1973) referred one specimen from Gorstian-Ludfordian Paadla Horizon and two specimens from the late Ludfordian Kuressaare Horizon to *E. confusum* (Počta).

Podolia

Bulvanker (1952) described *Xylodes nikiforovae* sp. nov. from the Malinovsty and Skala Horizons but this was later referred to *Spongophylloides* by Sytova (1968). We have compared specimens from the Gorstian lower part of the Malinovsty Horizon to *E. fasciculatum* Wedekind.

Poland

Rozkowska (1962) described *E. pseudodiantus* (Weissermel) from the upper part of the greywacke sequence of the lower Rzepin Beds in the Lezyce-Belczoross section in the Holy Cross Mountains. This unit equates with the lower Pridoli (Bassett *et al.* 1982), lowermost part of the Podlasie Horizon (Tomczyk 1970). The form may well belong to *Entelophyllum* but positive identification from available line drawings is not possible.

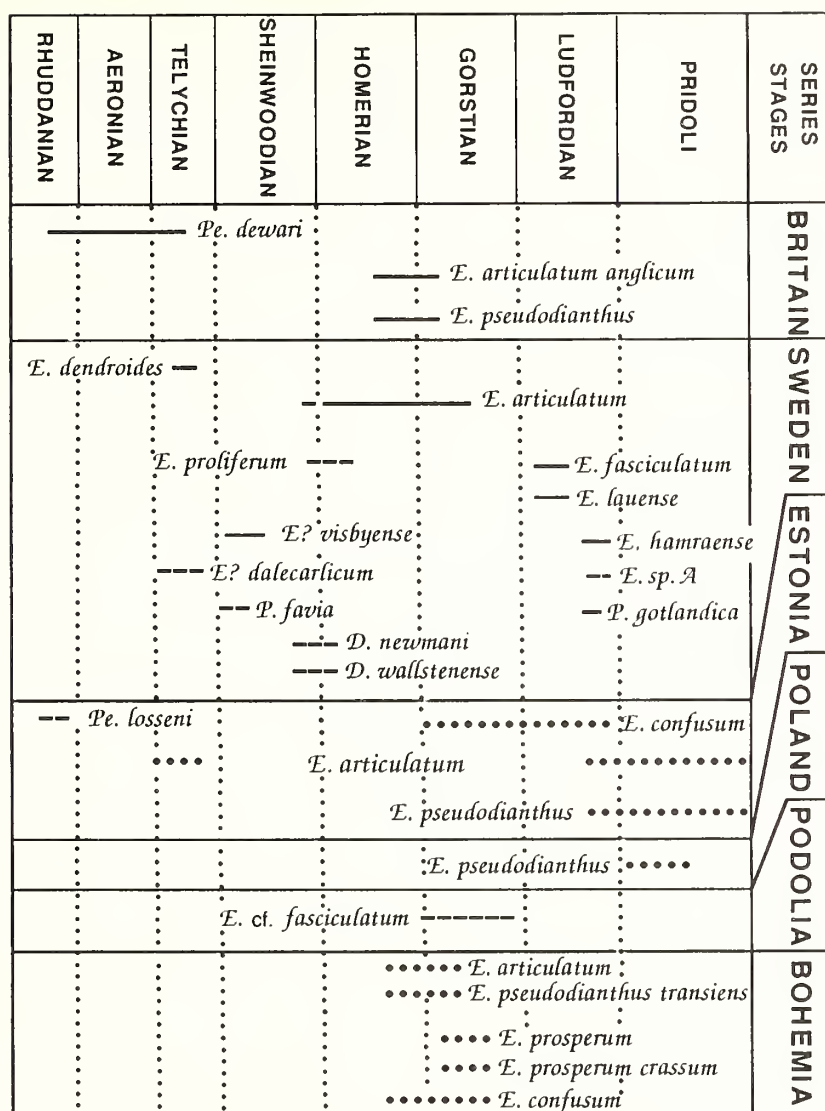
Czechoslovakia

Entelophylloid corals from Bohemia, first described by Počta (1902) and revised by Prantl (1940), are similar to the English *E. articulatum anglicum* – *E. pseudodiantus* forms and became even more carinate. Prantl (1940) recorded the less carinate *E. articulatum* and *E. pseudodiantus transiens* from the upper Motol Formation (Homerian) extending into the lower Kopanina Formation (Gorstian); specimens from the 'Amerika' quarries are now thought to be from the Kopanina Formation (Galle pers. comm.). *E. prosperum* and *E. prosperum crassum* are common in the Kopanina Formation. Prantl's material was from Tachlovice but today the precise locality is not known and it is thought to have been in a mine (Galle pers. comm.). *E. confusum* is known from the upper Motol and Kopanina Formations.

PHYLOGENY

In northern Europe, the earliest members of this group are referred to *Petrozium* (Text-fig. 3) and are characterized by a less well developed biserial tabularium than in later forms, and by stout straight long septa, and a relatively narrow dissepimentarium. The first species with a well-developed biserial tabularium occurs in the Telychian of Gotland but it still shows simple septa and a narrow dissepimentarium. Typical *Entelophyllum* is not known from the early Sheinwoodian of northern Europe.

E. articulatum with well developed long septa, biserial tabularium, and wide uniform



TEXT-FIG. 3. Stratigraphic distribution of species of *Entelophyllum* and related genera in northern Europe. Bold solid lines indicate confirmed identifications and stratigraphic ranges; bold dashed lines indicate confirmed identifications but stratigraphic ranges doubtful; dotted lines indicate identifications and stratigraphic ranges not confirmed by the authors.

dissepimentarium appears in the early Homerian in Gotland. It continues through the Gorstian and is thought to give rise to *E. fasciculatum* in the early Ludfordian, with the withdrawal of the septa from the axis, a reduction in the width of the dissepimentarium, an increase in the size of dissepiments, and a less well defined separation of axial and periaxial tabellae. The middle to late Ludfordian *E. lauense* and *E. hamraense*, with heavily carinate septa, possibly evolved from this stock. In England, *E. articulatum anglicum*, with light carination of some septa, occurs later in the Homerian than *E. articulatum articulatum* in Gotland. The English subspecies also dies out earlier

and again this may be related to changes in facies. In England, forms with different colony shapes and with strongly carinate septa, referred to *E. pseudodianthus* occur throughout the range of *E. articulatum anglicum*. Similar variation is found in the Bohemian forms of the *E. articulatum* – *E. pseudodianthus transiens* – *E. prosperum* – *E. prosperum crassum* group. Here they have a range slightly longer than the English forms but within the range of *E. articulatum* in Gotland. In contrast, the latter species is recorded in Estonia in Telychian as well as late Ludfordian and Pridoli intervals (Text-fig. 3). These presumed occurrences and others from elsewhere in the world may have had the name *E. articulatum* loosely applied.

Ceriod species with typical entelophylloid internal features (*Prohexagonaria favia* and *P. gotlandica*) occur at widely separated horizons on Gotland (Text-fig. 3). Whether these represent iterative evolution from the Baltic entelophylloid stock or successive migrations from an evolving *Prohexagonaria* lineage elsewhere, must await detailed study of *Prohexagonaria*.

Two new species of *Donacophyllum* in Gotland (Text-fig. 3) have similar internal features to *E. articulatum* but show non-parricidal rather than parricidal increase and commonly have well developed lonsdaleoid dissepiments. This generic similarity suggests affinities between Entelophyllidae and Kyphophyllidae.

PALAEOBIOGEOGRAPHY

The first occurrences of entelophylloid forms are from opposite sides of the Iapetus Ocean. In Llandovery times *Petrozium dewari*, from Girvan, Scotland, would have been on the southeastern seaboard of the North American Continent, and *P. losseni*, from Estonia, on the Anglo-Baltic Plate (Text-fig. 1b; Cocks and Fortey 1982). In later Llandovery times as the Iapetus Ocean closed *P. dewari* is known from England and the first species of *Entelophyllum* occurs in Gotland. Although on the same plate, England and Gotland were separated by a broad sea on the site of the earlier deep Tornquist's Sea. This probably led to differentiation of subspecies in *E. articulatum*, earlier development of carinate forms in Britain, and evolution of *E. fasciculatum* in Gotland. Bohemian and English forms show a similar development, reflecting the closer proximity of England to the northern Gondwanan Continent in the Llandovery as the Rheic Ocean opened.

SYSTEMATIC PALAEOONTOLOGY

Terminology and suprageneric classification follow Hill (1981). Measurements are standard, with the diameters of corallites being the mean of the diameters of the circumscribed and inscribed circles in transverse section.

Septal microstructure is similar in all species described. Septa are monacanthate with the monacanth arranged in broad half fans over the dissepimental floors and inclined upwards and inwards towards the axis in the tabularium. Monacanth vary from 0.01 to 0.02 mm in diameter and the fibres appear to diverge only slightly from the axis of the trabeculae. Thus axes of trabeculae and junctions between trabeculae are not obvious so that in median longitudinal section septa have a fibrous appearance (Pl. 1, fig. 2; Pl. 5, fig. 20).

Variation and taxa discrimination

Large samples of *E. articulatum anglicum* subsp. nov. and of *E. yassensis* (Etheridge) from Australia, to be described in a future paper, indicate considerable intra-colony and intra-specific variation. Previously, characters showing intra-colony variation have been used to differentiate species and even genera by some authors.

In *E. articulatum anglicum*, variation in colony form appears to be dependent on environmental conditions. Flattened colonies are most common in bedded limestones and marls, whereas tall globular heads are found in more massive biohermal limestones. Ranges of variation in corallite diameter and septal number are almost as great for the holotype (10–19 mm, 21–32 major septa) as for the populations from Dudley (twenty-four specimens: 8–19 mm, 21–32 major septa) and Wenlock Edge (forty specimens: 9–20 mm, 20–32 major septa). Mean colony corallite diameters are likewise variable but mean colony tabularium diameters remain fairly constant. There seems to be no relationship between corallite diameter or septal number and corallum form. Major septa are generally long, straight, smooth and extend to the axis, but within one corallum they may tend

to withdraw from the axis, become discontinuous at the periphery, and carry zigzag carinae. Discontinuity in the dissepimentarium appears to be connected with widening of the dissepimentarium associated with connecting processes. In several sections of one corallum, septal carination is confined to the oldest part of the corallite just before budding. However, in other specimens development of carinae is spasmodic throughout the corallite. In contrast, septal microstructure, tabularial characters, and dissepimentarium apart from its width, all show little variation.

E. pseudodianthus (Weissmerl), which occurs with and resembles *E. articulatum anglicum* typically but not invariably has heavily carinate septa. Similarly, on Gotland, most specimens of *E. fasciculatum* are readily distinguished from *E. articulatum* but in some colonies a few corallites show characters typical of the other species. The ranges of variation of these stratigraphically separated forms also show considerable overlap.

It is tempting, after admitting such considerable variation, to lump together all the above mentioned forms into one species. This would obscure the biostratigraphic and palaeogeographic usefulness of these groups of corals in northern Europe. Assignments are subjective and may well need future modification but they will provide a basis for the careful description of forms from elsewhere. Diagnoses formulated are for typical coralla and corallites within coralla, and the exceptions are noted but not included.

At generic level, the fasciculate and cerioid forms are differentiated, as are those with parricidal and nonparricidal colony increase. But even at this level intracolony variation has produced exceptions with some cerioid forms becoming locally fasciculate and some colonies with typical parricidal increase having one or two corallites that produced lateral nonparricidal offsets. *Petrozium* is retained for the simpler early forms without well-developed biserial tabularia and dissepimentaria, since it appears to have stratigraphic significance.

Synonymy

We have used many of the symbols proposed by Matthews (1973) to indicate degree of confidence in synonymy listings. These lists include only the most important previous citations, all of which we have examined and evaluated.

Collections

The repositories in which the material described herein is housed are indicated by the following prefixes: BMNH, British Museum (Natural History), London; BU, University of Bristol, Bristol; EGM, Eesti NSV Teaduste Akadeemia, Geoloogia Instituudi, Tallinn; GSM, Institute of Geological Sciences, Keyworth; NM, Národní Museum, Prague; OU, University of Oklahoma, Norman; RM, Paleozoologiska sectionen, Naturhistoriska Riksmuseet, Stockholm; SM, Sedgwick Museum, Cambridge; SMF, Natur-Museum Senckenberg, Frankfurt-am-Main; UB, University of Birmingham, Birmingham; UO, University of Oxford, Oxford; UQ, University of Queensland, Brisbane.

Subclass RUGOSA Milne-Edwards and Haime, 1850

Order STAURIIDA Verrill, 1865

Suborder ARACHNOPHYLLINA Zhavoronkova, 1972

Family ENTELOPHYLLIDAE Hill, 1940

Genus ENTELOPHYLLUM Wedekind, 1927

1927 *Entelophyllum* Wedekind, p. 11.

1927 *Xylodes* Lang and Smith, p. 461 (pre-occupied by *Xylodes* Waterhouse, 1876, a Recent coleopteran).

1944 *Stereoxylodes* Wang, p. 25.

1964 *Carinophyllum* Strelnikov, p. 59.

Type species. Chosen by subsequent designation of Lang *et al.* 1940, p. 57, *Entelophyllum articulatum* (Wahlenberg, 1821) from the Slite, Mulde, Klinteberg, and lower Hemse Beds of Gotland; Homerian to early Ludfordian Stages, late Wenlock to early Ludlow.

Diagnosis. Phaceloid or dendroid rugosans with peripheral parricidal increase; septa long, generally radially arranged, counter-cardinal septa rarely distinguishable, smooth or asymmetrically carinate; major septa slightly withdrawn from axis; minor septa contraclined or contratigent in some; tabularium wide, broadly domed commonly with depressed axial area and marginal periaxial

trough formed by small subhorizontal or concave tabellae; dissepiments numerous, small, globose with lonsdaleoid dissepiments in some.

Remarks. Wedekind placed eight species in *Entelophyllum*, but named no type species. Among these was *E. articulatum*, cited without any author's name or statement that it was new. Lang *et al.* (1940) considered that *Madreporites articulatus* Wahlenberg was implied, and with this we would agree. By selecting *E. articulatum* (Wahlenberg) as type, the invalid homonym *Xylodes* Lang and Smith became an objective synonym of *Entelophyllum*.

Soshkina and Dobrolyubova (1962, p. 333) listed *Evenkiella* Soshkina, 1955, as having *Madreporites articulatus* Wahlenberg as the type species, and gave *Xylodes* as a synonym. Soshkina (1955) had, however, named as type species of *Evenkiella* nom. nov., *Evenkiella helenae* Soshkina, 1955 (p. 126, pl. 13, fig. 1) from the Wenlock of the Stony Tunguska River, Siberia. In a footnote she explained 'name *Evenkiella* for the genus given instead of *Xylodes* Smith and Tremberth, previously used for an insect'. In our opinion the designation of *E. helenae* as type species is of stronger force than the citation 'nom. nov.' instead of 'gen. nov.' and the explanatory footnote, and we uphold *E. helenae* as type in spite of Soshkina and Dobrolyubova's later reference to *M. articulatus* as the type. We consider the cerioid *Evenkiella* distinct from *Entelophyllum* in that it has lonsdaleoid dissepiments, flat complete tabulae, septa composed of fine trabeculae, and we agree with its placement in the Kyphophyllidae by McLean and Pedder (1984, p. 18).

Stereoxylodes was proposed by Wang (1944) as a subgenus of *Entelophyllum*, with type *Cyathophyllum pseudodiantus* Weissmerl, 1894, for entelophyllids with dilated and carinate septa. The type specimen of *C. pseudodiantus* chosen by Lang and Smith (1927, p. 473) as the original of Weissmerl (1894, pl. 47, fig. 3) from the glacial drift of Lauth, Germany, is lost. Ivanovskii (1976, p. 165) invalidly proposed as a neotype of *E. pseudodiantus*, the holotype of *Stereoxylodes pseudodiantus* var. *sinensis* Wang, 1944 from the 'middle' Silurian of Malung, eastern Yunnan, China. To stabilize this species, we have selected a lectotype from Weissmerl's syntypes, see discussion of *E. pseudodiantus*. In England, *E. pseudodiantus* commonly occurs as small loose clumps of ceratoid corallites formed by peripheral parricidal budding and with strongly carinate and commonly thickened septa, quite distinct from the typical phaceloid coralla of *E. articulatum anglicum* with cylindrical corallites and typically little or only light carination of the septa. As described in detail later, some specimens of both species show variation that liken individual corallites or whole coralla to those of the other. Prantl (1940) also recognized a similar tendency and proposed *E. pseudodiantus transiens* for forms showing smooth, slightly carinate, dilated and asymmetrical carinate septa combining characters of *E. articulatum* and *E. pseudodiantus*. Similarly, Strelnikov (1964, p. 59) erected *Carinophyllum* for species that have septa thickened in the inner dissepimentarium and are heavily carinate, and designated *E. confusum* (Počta, 1902) as type species. Like Schouppé (1951), we believe that there is a continuum of variation in the thickening and carination of the septa in the dissepimentarium of such entelophylloid corals and that they all belong to the one group. They may be arbitrarily divided into subgenera but there does not appear to be any biogeographic or stratigraphic significance to such divisions. If such a subdivision was practical, then *Nanshanophyllum* Yu (1956; type *N. typicum* Yu, Middle Silurian, China) might be

EXPLANATION OF PLATE I

Figs 1–10. *Entelophyllum articulatum* (Wahlenberg). 1–6, RM Cn54823 (neotype), unknown horizon and locality on Gotland; 1, lateral view showing tall corallites, $\times 1$; 2 and 3, longitudinal sections showing typical biserial tabularium and small globose dissepiments, $\times 4$, $\times 2$, respectively; 4–6, transverse sections showing long smooth septa, $\times 2$, $\times 2$, $\times 4$ respectively. 7–10, Slite Beds, Bogeclint 1, 2 km SE of Boge church, Gotland; 7 and 8, UQ F34300; 7, longitudinal section, $\times 2$; 8, transverse section, $\times 2$; 9 and 10, UQ F34298; 9, longitudinal section, $\times 2$; 10, transverse section, $\times 2$.



regarded as another subgenus of the group for solitary forms with thickened and carinate septa, in the same way as Pedder (1976) used it as a subgenus of *Stereoxylodes*.

Although some species contain both cerioid and fasciculate forms (such as *E. polymorphum* Shurygina, 1977, pl. 6, figs 1–3 [= *E. articulatum* of Sytova 1952, p. 140, pl. 4, figs 1–5] from the 'upper' Silurian of the Urals), we refer typical cerioid species to *Prohexagonaria* Merriam, 1973 (see discussion of that genus).

We include in *Entelophyllum* only species that show parricidal budding. One apparent exception is *E. articulatum anglicum*. It almost invariably has obvious parricidal budding but we have observed one corallum, which, in addition to common parricidal budding, includes a single example of lateral budding. Similarly, lonsdaleoid dissepiments are uncommon in most species of *Entelophyllum* but do occur in some corallites in coralla of various species especially in areas of lateral outgrowths and in the late growth stages. Forms showing lateral budding and well-developed lonsdaleoid dissepiments are included in *Donacophyllum* Dybowski, 1874. The two species here included in it are similar to *Entelophyllum* in their septa and tabularia.

Entelophyllum articulatum (Wahlenberg, 1821)

Plate 1, figs 1–10; Plate 2, figs 1–11

- (1821) *Madreporites articulatus* Wahlenberg, p. 97.
- v*1837 *Cyathophyllum articulatum* (Wahlenberg); Hisinger, p. 102, pl. 29, fig. 4.
- 1874 *Cyathophyllum articulatum* (Wahlenberg); Dybowski, p. 435, pl. 3, fig. 1, 1a, 1b.
- 1927 *Entelophyllum articulatum* (Wahlenberg); Wedekind, p. 22.
- v1929 *Xylodes articulatus* (Wahlenberg); Smith and Tremberth, p. 363, text-figs 1 and 2; pl. 7, fig. 5 [non figs 1–4, 6].
- v1933 *Xylodes articulatus* (Wahlenberg); Smith, p. 513, pl. 1, figs 4 and 5 [non figs 1–3].
- 1940 *Entelophyllum articulatum* (Wahlenberg); Lang *et al.*, p. 57.
- (?)1940 *Xylodes articulatus* (Wahlenberg); Prantl, p. 6, pl. 1, figs 1–3; pl. 2, figs 1, 3, 4.

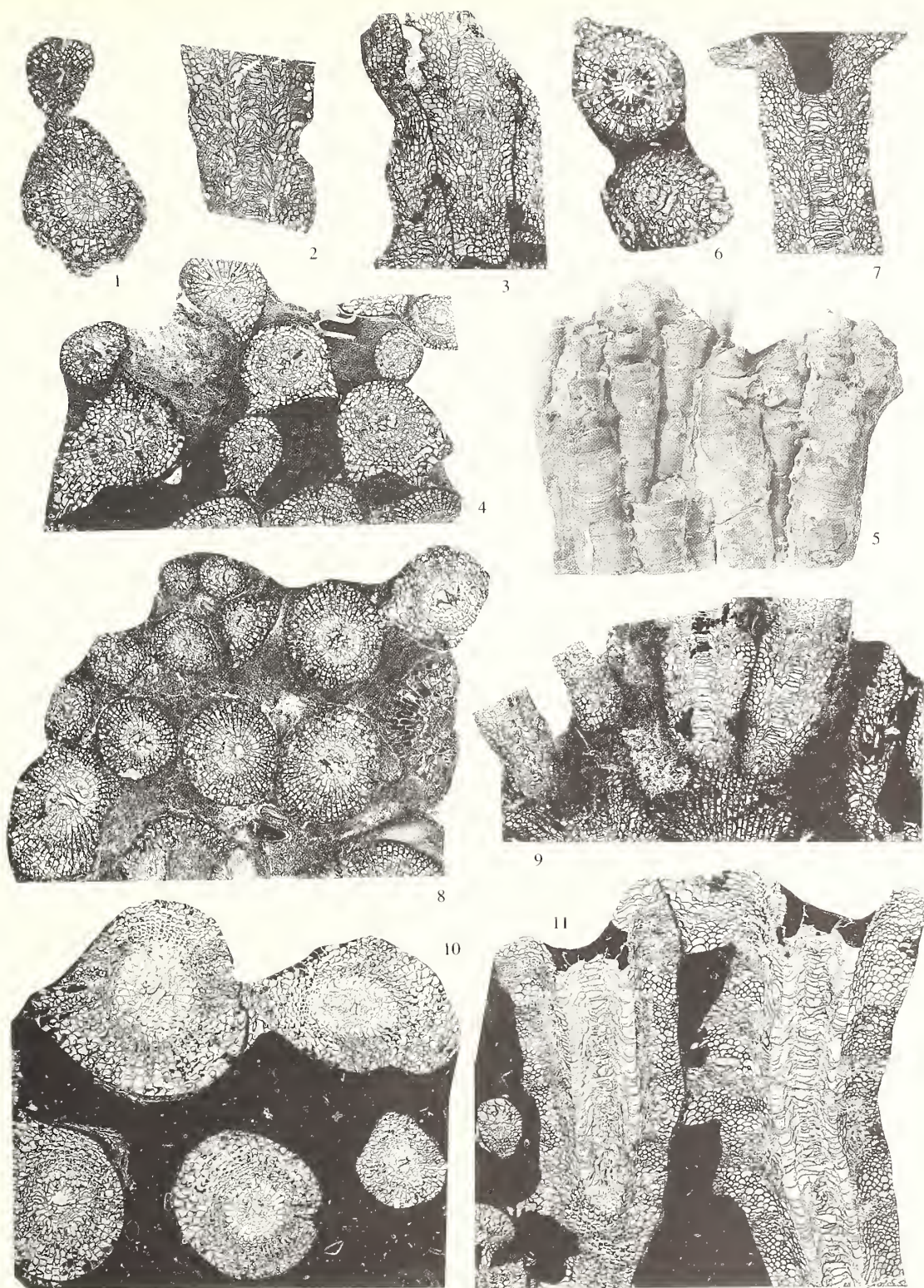
Neotype. Chosen by Smith and Tremberth (1929, p. 363), one of the original specimens of Hisinger labelled '*Cyathophyllum articulatum* e Gottlandia'; RM Cn54823, from an unknown locality and horizon on Gotland.

The exterior side view of the neotype was figured at half size by Smith and Tremberth (1929, p. 365, text-fig. 1). Three thin sections cut from the neotype with the numbers R49348*a*, *b*, and *c* are in the British Museum (Natural History). The two transverse sections, apparently cut from the base of the specimen, include two corallites each and there is a longitudinal cut from a single corallite, apparently from high on the side of the specimen. Smith and Tremberth (1929, p. 365, text-fig. 1) figured one of the four transverse corallites and Smith (1933, pl. 1, figs 4 and 5) refigured that picture and also figured the longitudinal section. At a later time two additional transverse sections were taken from the base of the neotype, which include two corallites each, and a longitudinal section was taken from one of these corallites. These sections carry the same number as the neotype, Cn54823, in the Riksmuseet, Stockholm (Pl. 1, figs 3–6).

Material studied. The neotype; similar material occurring in the Slite Beds at Bogeclint 1, northeast coast of Gotland (6 specimens; figured: UQ F34298, F34300). Other Gotland occurrences: upper Mulde Beds, from Blåhäll 1, on west coast of Gotland (one specimen; figured: RM Cn66044); Klinteberg Beds, from

EXPLANATION OF PLATE 2

Figs 1–11. *Entelophyllum articulatum* (Wahlenberg), showing variation in Gotland material. 1 and 2, RM Cn66040, Klinteberg Beds, Klinteberget 1, cliff exposure at Klinte, west coast of Gotland; 1, transverse section, $\times 2$; 2, longitudinal section, $\times 2$. 3–9, lower Hemse Beds, Snoder 1, 2.5 km NW of Slite Church, southwest Gotland; 3–5, RM Cn66041; 3, longitudinal section, $\times 2$; 4, transverse section showing lateral expansions of corallites, $\times 2$; 5, lateral view showing parricidal increase, $\times 1$; 6 and 7, RM Cn66042; 6, transverse section, $\times 2$; 7, longitudinal section, $\times 2$; 8 and 9, RM Cn66043; 8, transverse section, $\times 2$; 9, longitudinal section, $\times 2$. 10 and 11, RM Cn66044, upper Mulde Beds, Blåhäll 1, 0.5 km NE of Djupviks fiskage, west coast of Gotland; 10, transverse section, $\times 2$; 11, longitudinal section, $\times 2$.



Klinteberget 1, central western Gotland (seven specimens; figured: RM Cn66040); Lower Hemse Beds, from Snoder 1, southwest Gotland (four specimens: figured RM Cn66041, Cn66042, Cn66043).

Distribution. Gotland: Homeric and Gorstian; Estonia: ?Telychian to Pridoli; Bohemia: ?late Homeric to early Gorstian.

Diagnosis. Phaceloid, increase peripheral, parricidal; corallite diameter 10–15 mm. Major septa typically 23–28, long, thin, extending to or almost to axis, rarely irregularly zigzag to flexuose in outer dissepimentarium, rarely carinate; minor septa two-thirds the length of major, may be irregularly contratigent, Tabularium one-third to one-half diameter of corallite, distinctly biserial with well developed periaxial trough. Dissepiments small, globose, to medium and irregular in size.

Description. Coralla are typically large, tall and phaceloid. Corallites are subcylindrical, closely packed, sub-parallel and up to 16 mm in diameter with irregular growth contractions and expansions (Pl. 1, fig. 1). The neotype is a fragment about 130 mm in length and 50 mm in diameter (Pl. 1, fig. 1). It includes parts of four corallites that represent one generation, approximately 100 mm in length. At the top of the fragment ten corallites are to be seen. Increase is peripheral and parricidal with buds extending almost straight up from the dissepimental zone of the parent corallite. Commonly, budding is more frequent than in the neotype and the corallites are less than 100 mm in length.

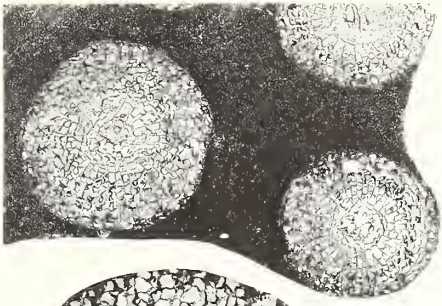
In transverse section major septa are typically long and thin but are highly variable even in the neotype. Major septa number 23–32 at diameters of 12–16 mm. Septa typically extend to the axial region but do not form an axial structure. A small open axial area about 1 mm in diameter occurs in some corallites. Most septa are thickened in the outer dissepimentarium and taper evenly towards the axis but in some corallites they thin in the tabularium to about half their thickness in the dissepimentarium. Some are irregularly zigzag to sinuous in the dissepimental area and are locally carinate. Some corallites show no carinae at all. Minor septa are about two-thirds the length of the major septa and commonly extend just past the inner margin of the dissepimental zone. However, in two specimens they are four-fifths the length of the major septa and extend into or across that part of the tabularium that forms the outer trough. Some minor septa are irregularly contratigent but they form no pattern. In some corallites, minor septa are discontinuous. In such cases, herringbone dissepiments are generally present. Locally, a few major and minor septa become discontinuous near the periphery and lonsdaleoid dissepiments are developed (Pl. 1, fig. 10). These discontinuous septa coincide with a lateral extension of the margin of the corallite that may represent a lateral outgrowth of attachment and the two developments are presumably related.

The tabularium is typically 4–5 mm in diameter. Longitudinal sections show two series tabellae (Pl. 1, figs 2 and 3; Pl. 2, fig. 11). Those in the axial region are generally flat but sag axially in those corallites with the septa slightly withdrawn from the axis, and have sharply downturned marginal edges. Between this zone and the dissepiments lies a narrow zone occupied by flat, sagging or inclined tabellae that number 5–8 in 5 mm vertical spacing, and form a periaxial trough. Small arched tabellae may be situated at the margins of the flat central region, forming levy-like margins to the central platform (Pl. 1, fig. 9). Dissepiments are small, globose, and form a wide peripheral zone that varies considerably in relative width as a result of rejuvenescence, from about one half to two-thirds the corallite radius. The number of rows of dissepiments varies from 3 to 12 and dissepiments are uniform in size and distribution and number 13–14 in 5 mm vertically.

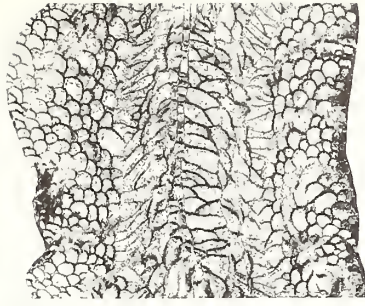
Remarks. In Gotland, *E. articulatum* occurs in the Slite, Mulde, Klinteberg and Lower Hemse Beds. Even in the Slite, in comparison with the neotype, some specimens have a comparatively narrower

EXPLANATION OF PLATE 3

Figs 1–10. *Entelophyllum articulatum anglicum* subsp. nov., showing variation in holotype, SM A5143, Much Wenlock (Dudley) Limestone, Dudley, Worcestershire. 1, transverse section of typical corallites, $\times 2$. 2 and 3, longitudinal sections, $\times 4$, $\times 2$ respectively. 4, transverse section showing corallite expansion, $\times 4$. 5, transverse section showing some septa slightly thickened and zigzag, $\times 4$. 6, transverse section of an early growth stage, $\times 4$. 7, lateral view of corallum, $\times 1$. 8, transverse section, showing lightly carinate septa, $\times 4$. 9, lateral view showing parricidal increase, $\times 2$. 10, transverse section in the distal part of corallum showing lonsdaleoid dissepiments, $\times 4$.



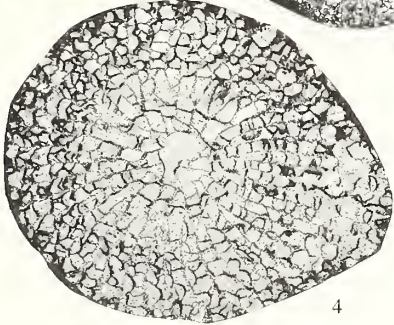
1



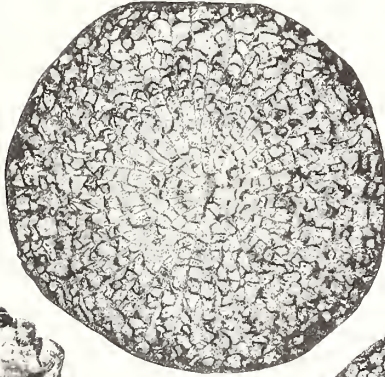
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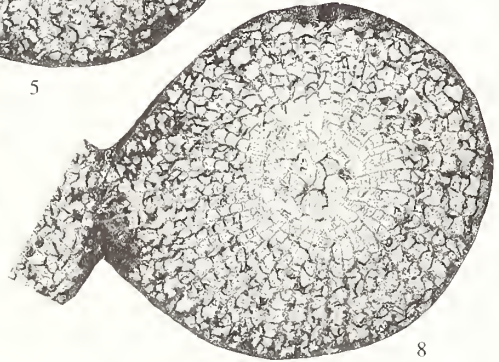
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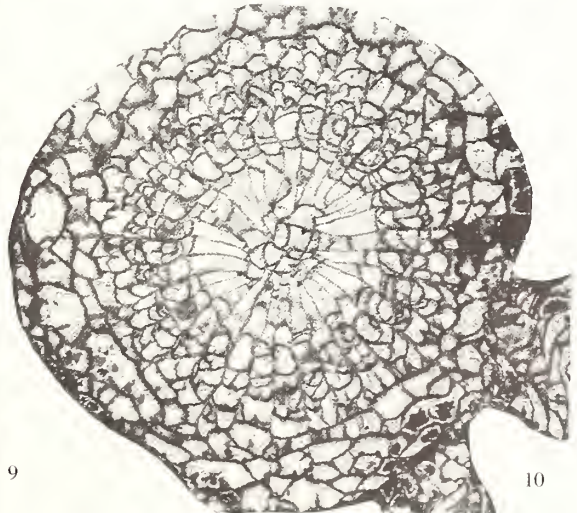
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9



10

dissepimental zone that includes some larger dissepiments (Pl. 1, fig. 9). Stratigraphically higher, budding patterns are more irregular, offsets are shorter, dissepiments are comparatively larger and more irregular in size, and septa tend to withdraw slightly from the axial region leaving a small open axial area. Beginning in the lower Hemse (Pl. 2, figs 2–4) there is an apparent shift in growth form in that there is a more frequent development of new parvicidal offsets but adult corallites remain typical.

Carinae are lacking in most specimens from Gotland. Where present they occur in the dissepimental zones of only a few septa. None of the specimens from Gotland develops complex vacuolar septa as occur in some corallites of the English subspecies *E. articulatum anglicum*.

In Estonia, Kaljo (1970) listed but did not describe or illustrate *E. articulatum* in coral faunas from the Adavere (Telychian), Kuressaare (late Ludfordian), Kaugatuma (early Pridoli) and Ohesaare (late Pridoli) Horizons (Text-fig. 2).

Smith and Tremberth (1929, p. 366) cited *E. articulatum* in the Upper Silurian of the Island of Bjerkøy, Christiania Fjord, Norway, but B. Neuman (pers. comm.) has been unable to find additional specimens in that area.

Smith and Tremberth (1929, p. 363) suggested that many Bohemian specimens (Počta 1902) figured as *Cyathophyllum prosperum* might be synonymous with *E. articulatum*. Prantl (1940) did not include any of Počta's figured material in *E. articulatum* but described *E. articulatum* from the 'Amerika' quarries, near Morina (Budnany). Dr A. Galle (pers. comm., 1989) considers these to be from the Kopanina Formation (Text-fig. 2). Occurrences in the Motol Formation (Prantl 1940) need to be confirmed. The septa are smooth, straight, extending almost to the axis and the tabularium and dissepimentarium are very similar to the Gotland material.

Material from the USSR, China, and Middle East, in Llandovery to Early Devonian strata, previously referred to *E. articulatum*, will now have to be reinterpreted.

Entelophyllum articulatum anglicum subsp. nov.

Plate 3, figs 1–10; Plate 4, figs 1–11

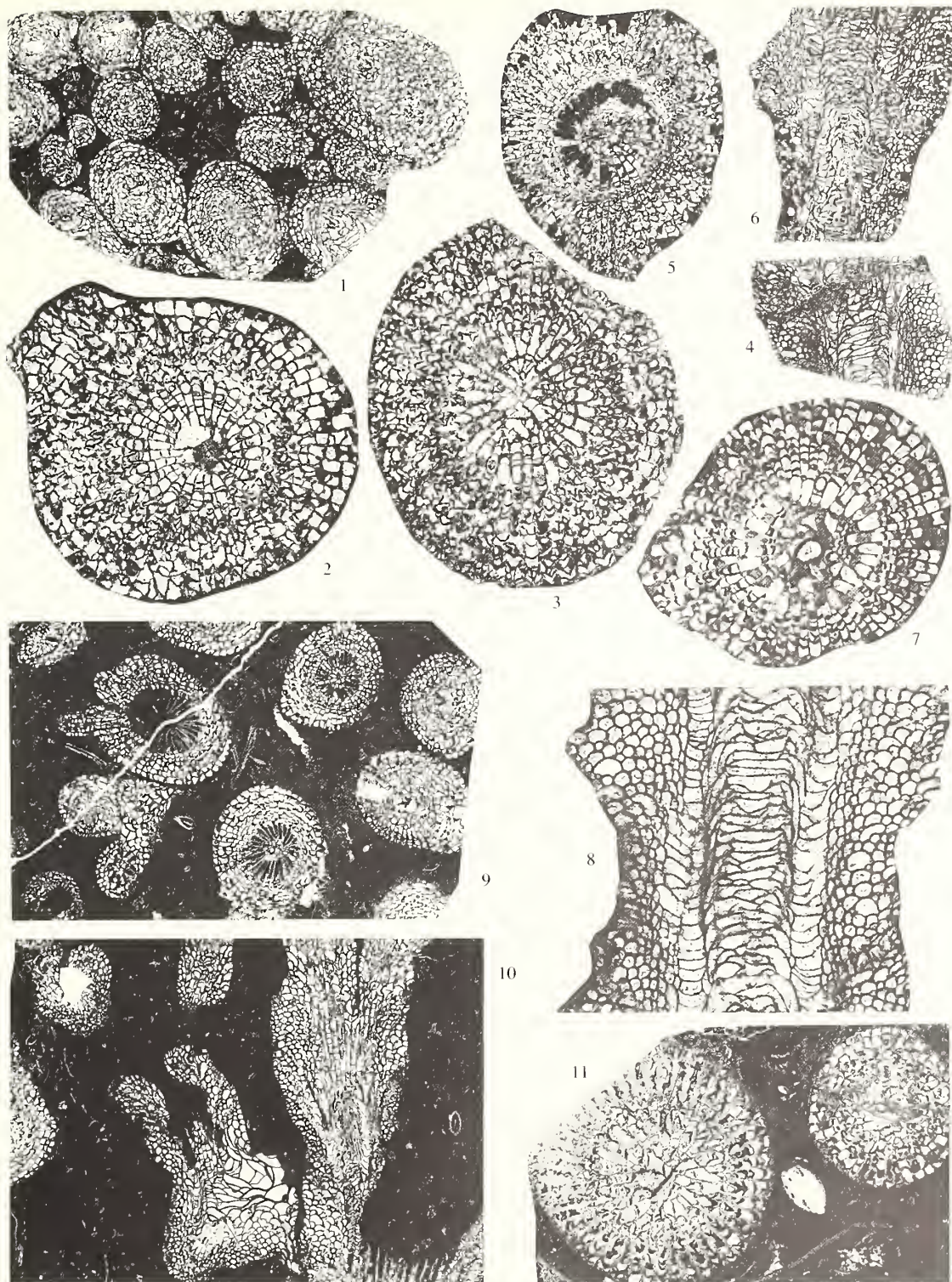
- v*1855 *Cyathophyllum articulatum* (Wahlenberg); Milne-Edwards and Haime, p. 282, pl. 67, fig. 1, 1a.
v1929 *Xylodes articulatus* (Wahlenberg); Smith and Tremberth, 1929, p. 363, pl. 7, figs 1–4, 6; pl. 8, fig. 2 (non pl. 7, fig. 5).

Holotype. Milne-Edwards and Haime, 1855, pl. 62, fig. 1, 1a; SM A5134a and thin sections SM A5134b–j from the Fletcher Collection, Much Wenlock (Dudley) Limestone, Dudley, Worcestershire; Homerian Stage.

Material studied. We examined sixty-four sectioned specimens from the collections of the BMNH, SM, UO, UB, and UQ from the Much Wenlock Limestone at Dudley, Worcestershire, and along Wenlock Edge, Shropshire; figured: SM A5134 (holotype), UQ F35311, F35315, F35319, F36966. Other English occurrences: Farley Member, Coalbrookdale Formation, Wenlock Edge (figured: UQ F41347); lower Elton Beds, Leintwardine, Shropshire; several specimens labelled lower Elton Beds, Wenlock Edge; several specimens labelled lower Ludlow (presumably Elton Beds), Ledbury Quarry, Malvern, Herefordshire.

EXPLANATION OF PLATE 4

Figs 1–11. *Entelophyllum articulatum anglicum* subsp. nov. showing variation in English material. 1–4, UQ F55311, Much Wenlock (Dudley) Limestone, Dudley, Worcestershire; 1–3, transverse sections, $\times 2$, $\times 4$, $\times 4$, respectively; 4, longitudinal section, $\times 2$. 5 and 6, UQ F41347, Farley Member, Coalbrookdale Formation, Presthope tunnel cutting, Wenlock Edge, Shropshire; 5, transverse section showing lateral dissepiments, $\times 2$; 6, longitudinal section, $\times 2$. 7 and 8, UQ F35315, Much Wenlock Limestone, Wenlock Edge, Shropshire; 7, transverse section, $\times 4$; 8, longitudinal section, $\times 4$. 9–11, Much Wenlock Limestone, Lilleshall Quarry, Wenlock Edge, Shropshire; 9 and 10, UQ F36966; 9, transverse section, $\times 2$; 10, longitudinal section, $\times 2$; 11, UQ F35319, transverse section showing thickened and carinate septa, $\times 4$.



Distribution. England: middle Homerian to early Gorstian.

Diagnosis. Coralla tall phaceloid to squat fasciculate; increase typically peripheral parvicidal; corallite diameter typically 10–12 mm, maximum 20 mm; major septa 21–24, maximum 30, straight to flexuose, smooth in tabularium, commonly reaching axis but not confluent; septa vary from straight, smooth or slightly thickened to zigzag and distinctly carinate, becoming very ragged and interrupted by lonsdaleoid dissepiments in the lateral expansions; minor septa commonly contraclined to contratigent around an obscure cardinal-counter plane. Tabularium biserial with well developed periaxial trough; dissepiments small, globose, regularly arranged in 5–8 vertical rows.

Description. Colony form varies from small clump-shaped coralla, 60 mm high and 40–45 mm in diameter showing two generations of budding, to squat or flat cake-shaped coralla several times greater in diameter than in height, up to 300 mm diameter, to tall large globular heads up to 1 m diameter. The holotype is a fragment of a tall, phaceloid colony 160 × 80 mm in cross section and 130 mm in height (Pl. 3, fig. 7).

Protocorallites, where preserved, vary from low petalate, up to 35 mm in diameter, to tall ceratoid corallites, 15 mm in diameter and 80 mm tall. Six to ten buds are generally produced at the first generation. In most coralla, budding occurs at the same level throughout the colony with the corallites in each generation being of the one length. In flattened colonies divergence of daughter corallites from the axis of the parent is rapid. In several flattened colonies growth increases on one side of the corallum. Budding is parvicidal but in two cases, UB 42 of Holcroft Collection and UQ F36996, it is nonparvicidal. Corallum increase appears to be peripheral, with one to six daughter corallites originating in the peripheral parts of the parent corallite generally at an expansion. The buds abruptly expand so as to occupy most of the calyx of the parent. Thin sections show buds originating at or just axial to the dissepimentarium/tabularium boundary.

Corallites are long, slender, cylindrical, and closely spaced, up to 10 mm. Corallites show regular contractions and expansions (Pl. 3, fig. 11). At intervals, a corallite may expand laterally to abut onto an adjacent corallite forming a connecting process 5–10 mm high. This pattern of outgrowths is not regularly spaced or level specific within a colony. Thus in transverse section the corallites show considerable variation in diameter (8–20 mm) but are commonly 10–13 mm. In the holotype first generation corallites are 20–30 mm long, those of the second 50–60 mm, and of the third 50–80 mm.

Septa are typically long and radially arranged in two orders (Pl. 3, fig. 1); one order commonly has 21–24 septa in adult stages at diameters 10–13 mm. At diameters 17–20 mm, major septa number 28–32. Major septa typically almost reach the axis; in some corallites an open axial area may be 1–2 mm in diameter (Pl. 3, figs 4–6). In a few corallites axial ends of the major septa deflect towards the cardinal-counter plane and the counter-cardinal septa may bisect the axial space. In others axial ends may be irregularly twisted. Minor septa are 0.6–0.8 of major septa and extend a short distance into the tabularium. Some minor septa may be contraclined and even contratigent. Septa are smooth and straight, curved or flexuose in the tabularium but are rather variable in the dissepimentarium even within one corallite. They may be straight or flexuose with smooth, rough or ragged sides (Pl. 3, fig. 8); slightly thickened at the junction of the septa with the curved dissepimental plates and carrying irregular zigzag carinae (Pl. 3, fig. 5); thickened in the inner dissepimentarium and outer tabularium so that they are fusiform (Pl. 4, fig. 11); or uncommonly discontinuous with irregular segments being interrupted by lonsdaleoid dissepiments (Pl. 3, fig. 10). Discontinuity of septa in the peripheral parts occurs in areas of broad expansion of the dissepimentarium (i.e. in a connecting process or just before budding). Septa may become more ragged or carinate in the expansions (Pl. 4, fig. 2).

The tabularium is relatively constant in diameter in adult stages, being 0.6 the corallite diameter. It shows an irregular separation into an axial series and a periaxial series of tabellae (Pl. 3, fig. 2). The axial series forms tabularial floors that are flat or slightly sagged axially and with steep downturned marginal slopes. Between this zone and the dissepimentarium is a periaxial series of flat, slightly sagging, or inclined tabellae (up to 30 per 10 mm vertically) forming a periaxial trough of the tabularial floors. The dissepimentarium varies in width as a result of the contractions and expansions of the corallite. Dissepiments are small, globose, and uniform in size and distribution (20–28 in 10 mm vertically and 6–8 total rows horizontally).

New offsets arise (BMNH R267) from the outer half of the periaxial series of tabellae and the axial edge of the dissepimentarium. The buds arise within the interseptal loculi between major and minor septa and thus budding is marginal and not truly tabularial. Having developed in the inner part of the marginarium they diverge towards the periphery and increase rapidly occupying the total dissepimentarium.

The twenty-five peels from UQ F36996 show close relationship between carinae and stages of parvicidal

increase. In this corallum, growth of a corallite stops when offsets develop. The septa are simple during growth but, near the base of the calice, just before budding occurs, septa become thickened, develop rough margins, become zigzag, and develop rudimentary, short carinae. New offsets almost invariably have simple thin septa in their early stages of growth. Earlier development of carinae is seen in some corallites in other coralla where they are not related to the development of offsets. In UQ F8388B, an individual corallite 50 mm in length has simple septa in the earliest stage, then carinate septa in a section 10 mm higher, then simple septa still higher, followed in the highest growth stages by the development of carinate and complex septa with vacuoles. Most of the other corallites in this same corallum have simple septa throughout their growth.

Remarks. *Entelophyllum articulatum anglicum* subsp. nov. is close to *E. articulatum* (Wahlenberg, 1821) from Gotland and many corallites cannot be differentiated. With sufficient material *anglicum* is seen to have more commonly carinate septa. Both subspecies show parricidal budding but in *anglicum* tabularia of the offsets may originate from the peripheral trough of the parent as illustrated by Smith and Tremberth (1929, text-fig. 2a), whereas in *articulatum* the indications are that offsets arise from wholly within the dissepimentarium. Minor differences are the more frequent occurrence among the English specimens of contratigent minor septa, development of an obscure cardinal-counter plane and less frequent development of discontinuous minor septa and lonsdaleoid dissepiments. Sections of *E. articulatum anglicum* showing more carinate septa resemble *E. pseudodiantlus* (Weissermel, 1894).

Entelophyllum fasciculatum Wedekind, 1927

Plate 5, figs 1–21

- v1927 *Entelophyllum fasciculatum* Wedekind, p. 24, pl. 2, figs 11 and 12; pl. 29, figs 30, 31, 50; ?pl. 29, figs 34–49, 51 [not sectioned]; ?pl. 30, figs 1–8 [not sectioned].
- v1927 *Entelophyllum proliferum typus* Wedekind, p. 23, pl. 29, figs 21 and 22 [*non* *Cyathophyllum proliferum* Dybowski, 1874, p. 445, pl. 3, fig 2a, b].
- v1927 *Entelophyllum proliferum* var. *elongata* Wedekind, p. 23, pl. 29, fig. 23; ?pl. 29, figs 24, 25, 33 [not sectioned].
- v1927 *Entelophyllum proliferum* var. *brevis* Wedekind, p. 23, pl. 29, figs 27 and ?28; ?pl. 29, figs 26 and 29 [not sectioned].
- non 1927 *Entelophyllum culmiforme* Wedekind, p. 23, pl. 29, fig. 32 [= tryplasmid coral].
- vp1927 *Entelophyllum roemeri* Wedekind, p. 23, pl. 30, fig. 15; ?pl. 30, figs 9–12, 16 [not sectioned] [*non* pl. 30, figs 13 (= holotype of *E. roemeri*) or 14 (both specimens = tryplasmid corals)].
- ?1927 *Entelophyllum rhizophorum* Wedekind, p. 23, pl. 30, fig. 17.
- ?1927 *Entelophyllum confer rhizophorum* Wedekind, p. 23, pl. 29, figs 18–20 [not sectioned].
- ?1973 *Entelophyllum articulatum* (Wahlenberg); Fedorowski and Gorianov, p. 19, pl. 4, figs 1–4.

Lectotype. Here chosen, original of Wedekind, 1927, pl. 29, fig. 30; RM Cn54855, *Rhizophyllum* limestone, lower Eke Beds, Lau Backar 1, southeast Gotland; middle Ludfordian Stage.

Material studied. All of Wedekind's (1927) original specimens of *E. fasciculatum* were from Lau Backar 1, southeast Gotland. Additional material examined by us from this locality are in the RM, UQ, OU, and Dr B. Neuman's collections. Sectioned specimens examined from Lau Backar number about thirty-five (figured specimens: RM Cn54855 (lectotype); RM Cn54847, Cn54849, Cn54850, Cn54852, Cn54856, Cn54880, Cn54881). The species also occurs at the same approximate horizon at Hallsarve 1, 0.4 km east of Lau Backar (figured RM Cn66045); Kauparvegård 1, inland cliff north of Kauparve farmhouse, southern Gotland; and possibly from an unknown locality, Östergarn parish, central east coast of Gotland.

Distribution. Gotland: middle Ludfordian.

Diagnosis. Phaceloid, increase peripheral, parricidal; corallite diameters 10–12 mm. Major septa typically 20–22, extending into tabularium but not reaching axis, leaving distinct open area in axial region. Septa typically straight throughout, not zigzag or carinate. Tabularium about one-half diameter, flat axially, sharply downturned to margin of dissepimentarium producing irregular periaxial trough. Dissepiments variable in size, width of zone medium.

Description. Specimens available include fragments of loosely dendroid to phaceloid coralla and numerous loose broken offsets. The latter are 30–70 mm long and ceratoid to cylindrical. Narrow distal ends of some loose offsets are turned abruptly laterally representing areas of attachment to parent. Increase is peripheral and parricidal with 4–6 offsets in each generation but 7 have been observed. Calices are shallow consisting primarily of a flat-bottomed axial pit coinciding with the tabularium and a marginal platform.

Septa typically number 20–22 of each order at diameters of 10–11.5 mm. Septa are relatively thin being thicker in the dissepimentarium compared to the tabularium. Septa are variable in the dissepimentarium. Most are straight and smooth, others are zigzag to sinuose. Isolated carinae are rarely developed in the zigzag septa of some specimens. Septa become discontinuous in the dissepimental zone only near a lateral extension (Pl. 5, fig. 5). Major septa are irregular in length and are 0.7–0.8 corallite radius in length leaving an open axial space up to 2 mm in diameter. Protosepta are not distinguishable and fossulae are not present. Minor septa are irregular in length and extend past the inner margin of the dissepimental zone.

The tabularium occupies half the corallite diameter. It consists of a broad axial region in which the tabulae are flat or with a wide, shallow median depression and a narrow periaxial region where edges of the tabulae are irregularly turned sharply down and in some cases back up again. Thus, an irregular periaxial trough may be developed that may contain a few horizontal tabellae (Pl. 5, fig. 20). Axial tabulae are irregularly spaced (12–16 vertically in 5 mm). The dissepimentarium is irregular due to variation in size and convexity of medium to large globose dissepiments that develop between the septa. There are 4–6 rows of dissepiments in a zone typically 3–4 mm in diameter and there are 8–10 in 5 mm vertically.

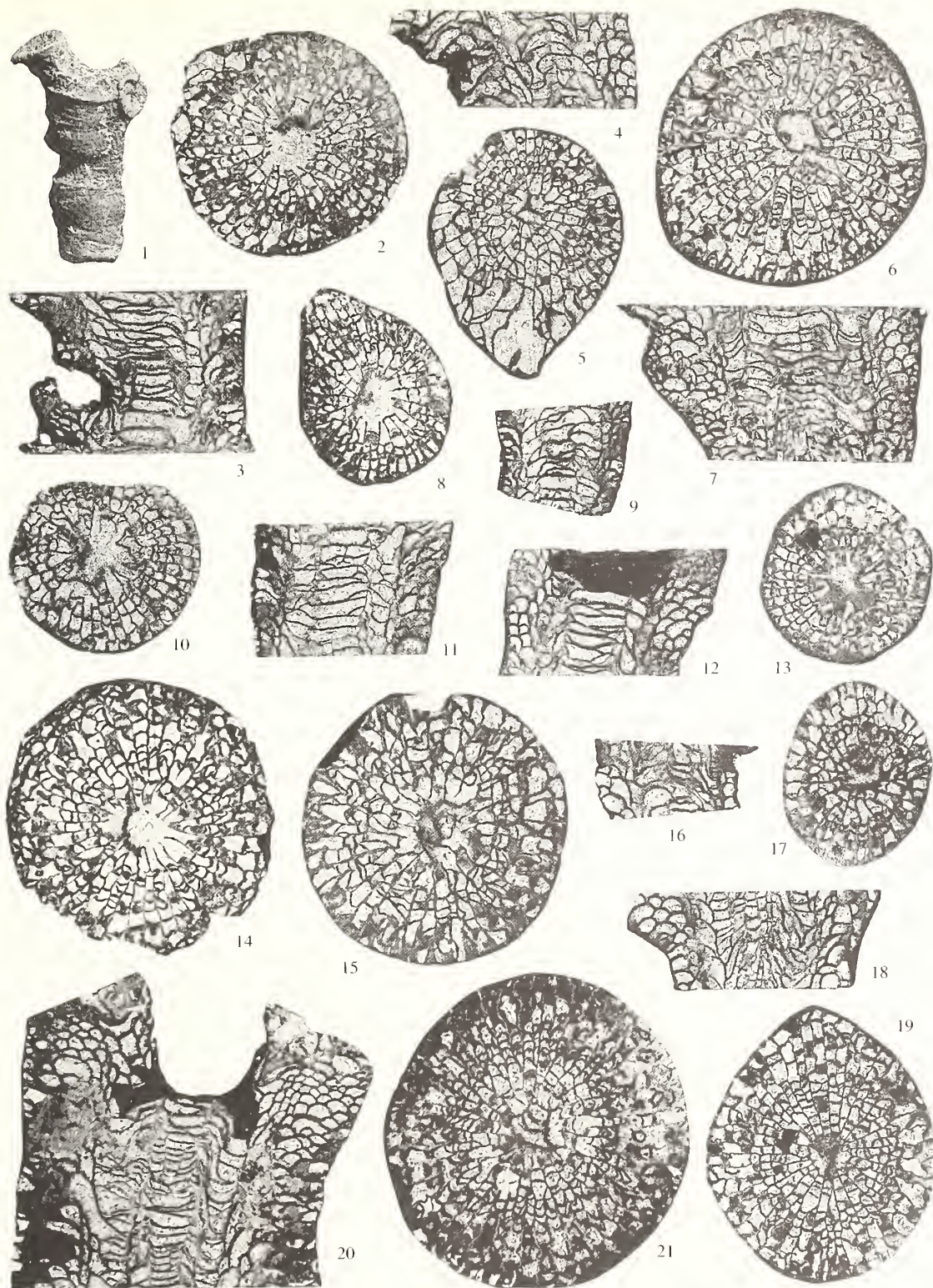
Remarks. *E. fasciculatum* apparently evolved in the Gotland area from *E. articulatum*. The former, in its common occurrences in the Upper Hemse/Lower Eke differs from forms similar to the neotype of *E. articulatum* in the Slite Beds in having a distinctly narrower dissepimental zone of relatively larger and more irregular globose dissepiments, in having septa withdrawn from the axial region, and in having a poorly defined separation of the tabularium into two zones with a less distinctly developed periaxial trough. However, *E. articulatum* in the Klinteberg and lower Hemse is similar to *E. fasciculatum* with which it could be considered to be gradational, but it has distinctly more open axial area and less well defined periaxial tabular trough.

Wedekind (1927) confused his definition of *E. fasciculatum* by basing the species primarily on the growth form of unsectioned broken offsets. He illustrated only two transverse sections. Also, he named as new (from the same locality, Lau Backar 1) an additional five species and varieties, all based on unsectioned broken offsets. The holotype or at least one syntype of each of these has been subsequently sectioned. Each of the following specimens is here named lectotype of the listed subspecies or variety of Wedekind (1927) and placed in the synonymy of *E. fasciculatum*:

EXPLANATION OF PLATE 5

Figs 1–21. *Entelophyllum fasciculatum* Wedekind. 1–19, *Rhizophyllum* limestone, Eke Beds, Lau Backar 1, 1.0 km NE of Lau, southeast Gotland; 1–3, RM Cn54855 (lectotype), original of Wedekind (1927, pl. 29, fig. 30); 1, lateral view; 2, transverse section; 3, longitudinal section; 4 and 5, RM Cn54852, original of Wedekind (1927, pl. 29, fig. 50); 4, longitudinal section; 5, transverse section; 6 and 7, RM Cn54857, original of Wedekind (1927, pl. 30, fig. 17), holotype of *E. rhizophorum* Wedekind; 6, transverse section; 7, longitudinal section; 8 and 9, RM Cn54853, original of *E. roemeri* Wedekind (1927, pl. 30, fig. 15); 8, transverse section; 9, longitudinal section; 10 and 11, RM Cn54856, original of Wedekind (1927, pl. 29, fig. 3); 10, transverse section; 11, longitudinal section; 12 and 13, RM Cn54849, original of Wedekind (1927, pl. 29, fig. 23), lectotype of *E. proliferum elongata* Wedekind; 12, longitudinal section; 13, transverse section; 14, RM Cn54881, original of Wedekind (1927, pl. 2, fig. 12), transverse section; 15, RM Cn54880, original of Wedekind (1927, pl. 2, fig. 11), transverse section; 16 and 17, RM Cn54850, original of Wedekind (1927, pl. 29, fig. 27), lectotype of *E. proliferum brevis* Wedekind; 16, longitudinal section; 17, transverse section; 18 and 19, RM Cn54847, original of Wedekind (1927, pl. 29, fig. 21), lectotype of *E. proliferum typus* Wedekind; 18, longitudinal section; 19, transverse section. 20 and 21, RM Cn66045, Eke Beds, Hallsarve 1, 1.35 km NE of Lau, Gotland; 20, longitudinal section; 21, transverse section.

All $\times 4$, except Fig. 1 which is $\times 1$.



1. *Entelophyllum proliferum typus* Wedekind, 1927, pl. 29, fig. 21 (RM Cn54847) (= Pl. 5, figs 18 and 17).
2. *E. proliferum* var. *elongata* Wedekind, 1927, pl. 29, fig. 23 (RM Cn54849) (= Pl. 5, figs 12 and 13).
3. *E. proliferum* var. *brevis* Wedekind, 1927, pl. 29, fig. 27 (RM Cn54850, = Pl. 5, figs 16 and 17).

The following specimens are tryplasmid corals and they must be transferred from *Entelophyllum*:

1. *Entelophyllum culmiforme* Wedekind, 1927, pl. 29, fig. 32 (RM Cn54854, holotype).
 2. *E. roemeri* Wedekind, 1927, pl. 30, fig. 13 (RM Cn54858, holotype), fig. 14 (RM Cn54859).
- Specimen RM Cn54853, the original of *E. roemeri* Wedekind, 1927, pl. 30, fig. 15, is referable to *E. fasciculatum* (= Pl. 5, figs 8 and 9).

The holotype of *E. rhizophorum* Wedekind (1927, pl. 30, fig. 17; RM Cn54857, = Pl. 5, figs 6 and 7) is questionably placed in the synonymy of *E. fasciculatum* as it is slightly larger and has some carinae. It is from Östergarn but the exact stratigraphic horizon is not known in the Hemse Beds and could be equivalent to or slightly older than Lau Backar 1. Wedekind (1927, pl. 29, figs 8–20) compared three specimens from Lau Backar to this species but the internal structures of these are still unknown.

Eichwald (1861) described but did not illustrate specimens from Estonia that he referred to *E. articulatum*. In their revision of Eichwald's collection, Fedorowski and Gorianov (1973) listed twenty-two specimens as *E. articulatum* (Wahlenberg) and figured two from the Paadla Horizon (Gorstian to early Ludfordian), one from the Kuressare Horizon (late Ludfordian) and one from the Kaugatuma Horizon (Pridoli), all from the Island of Saaremaa. From their description and illustrations (Fedorowski and Gorianov 1973, pl. 4, figs 1–4) these Eichwald specimens appear to compare more closely with *E. fasciculatum* in the smaller corallite size, smaller average number of septa, the development of a small open axial area, and the more common development of lonsdaleoid dissepiments that are larger and more irregular in size. The two figured longitudinal sections (Fedorowski and Gorianov, pl. 4, figs 3*b* and 4*b*) are not median and it is difficult to compare their tabularia with those of the Gotland material.

Entelophyllum cf. *fasciculatum* Wedekind, 1927

Text-fig. 4A–F

Material studied. Material given to us at the Geological Institute in Kiev collected from the lower part of the Malinovtsy Horizon, Grate Sloboda, Dnister River, Podolia (four specimens; figured: OU 10668–10671).

Distribution. Podolia: Gorstian Stage.

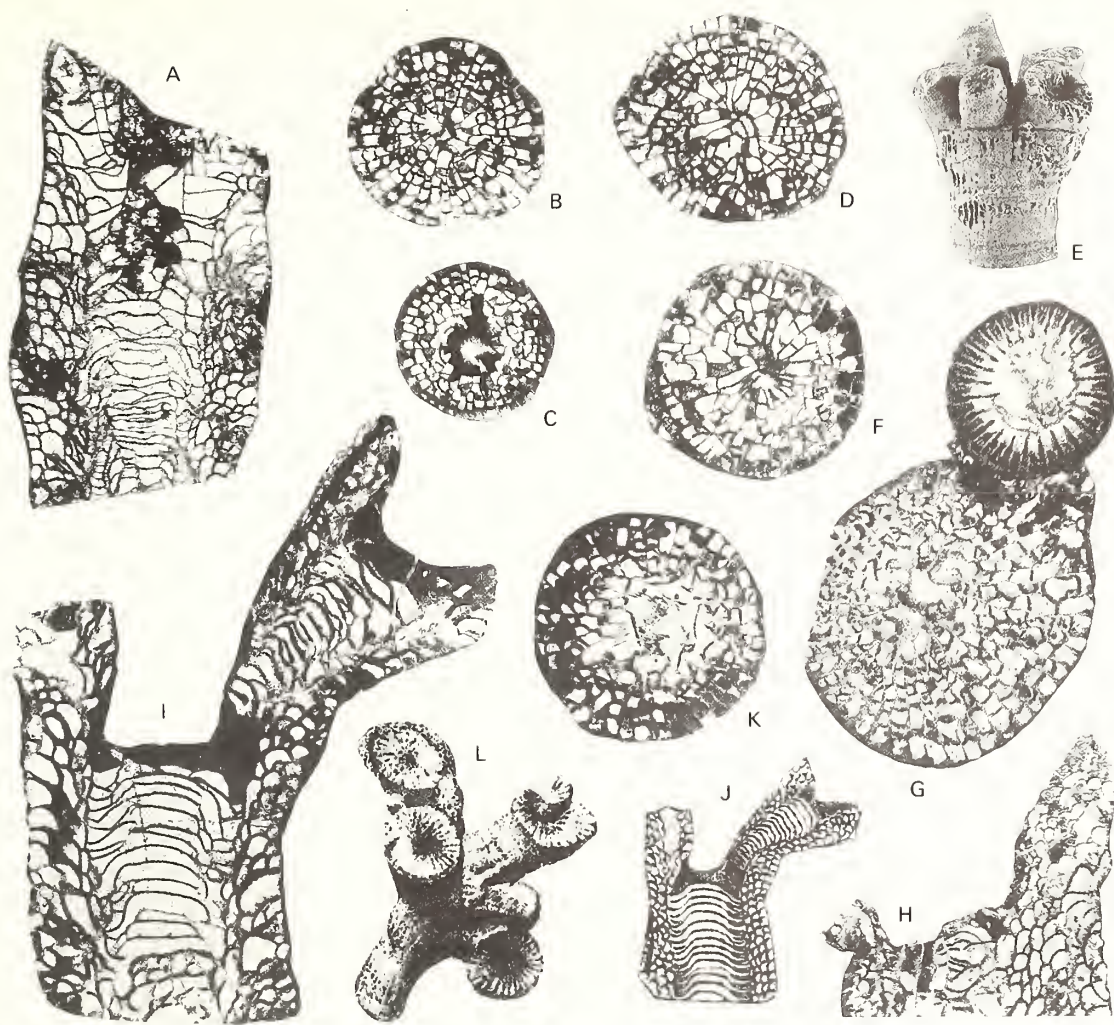
Description. Cylindrical corallites 6–8 mm in diameter and up to 25 mm in length. Two show peripheral parricidal increase with four and five offsets arising from the calical platform of the parent (Text-fig. 4E).

Septa are radially arranged with 22–24 in each order. Major septa are irregularly withdrawn from the axis leaving a distinct axial space. In the tabularium septa are thin, smooth and typically straight. They thicken in the dissepimentarium where they may be zigzag and carry rare carinae. Minor septa are typically 0.6–0.8 as long as the major but may be less than 0.3 or may be discontinuous being interrupted by larger interseptal dissepiments.

The tabularium is half corallite diameter. It consists of either complete tabulae that are strongly arched with flattened axial region and upturned peripheral edges, or more commonly closely spaced flat axial tabellae downturned sharply at their margins to rest on the ones below or supplemented by globose tabellae, with the space between the downturned edges and the dissepimentarium spanned by flat or concave tabellae.

Dissepiments are globose, vary from small to large, and are not arranged in vertical rows (Text-fig. 4A). In longitudinal section, offsets appear to be initiated in the periaxial trough of the tabularium and then expand with the dissepimentarium of the parent being reduced and the tabularium of the offset expanding outwards (Text-fig. 4A).

Remarks. Material from Podolia resembles *E. fasciculatum* from Gotland in having relatively simple



TEXT-FIG. 4. A-F, *Entelophyllum* cf. *fasciculatum* Wedekind, lower part of Malinovtsy Horizon, Grate Sloboda, Dnister River, Podolia; A and B, OU 10668; A, longitudinal section showing offset in top left corner, $\times 4$; B, transverse section, $\times 4$; C, OU 10669, transverse section, $\times 4$; D, OU 10670, transverse section $\times 4$; E and F, OU 10671; E, lateral view showing peripheral parricidal increase, $\times 2$; F, transverse section, $\times 4$. G and H, *Entelophyllum* sp. A., Hamra Beds, Kättelviken 3, coast below the road at Kättelviken, 3.5 km N of Hoburgen, southern tip of Gotland; G, transverse section abutting a tryplasmid corallite, $\times 4$; H, longitudinal section, $\times 4$. I-L, *Entelophyllum proliferum* (Dybowski), EGM Co1352 (lectotype), Slite Beds, Stora Karlsö, Gotland; I, longitudinal section showing offset, $\times 4$; J, reproduction of Dybowski (1874, pl. 3, fig. 2a), line drawing of longitudinal section, $\times 2$; K, transverse section, $\times 4$; L, reproduction of Dybowski (1874, pl. 3, fig. 2), showing corallum, $\times 2$.

septa withdrawn from the axis, a wide tabularium with a moderately developed periaxial trough, and irregular sized dissepiments. It differs in that the corallites are slightly narrower, more cylindrical, and the offsets do not diverge outwards from the lip of the parent calice as abruptly as in *E. fasciculatum*. Our material closely resembles material from Podolia in Dr V. A. Sytova's collection, which we examined in Leningrad, which she had tentatively referred to *E. proliferum* (Dybowski). Her material showed slightly more variation with one corallite having 30 major septa, and the septa slightly more thickened. The material from Podolia is certainly like the holotype of

E. proliferum (Text-figs 4i–l) but the latter species is known only from the one specimen from the Slite Beds of Stora Karlsö, Gotland and its range of variation is unknown. *E. proliferum* may be a senior synonym of *E. fasciculatum*.

Material from Podolia is similar to *Petrozium losseniformis* Zheltonogova (1965, p. 41, pl. 8, fig. 2) from the Gorstian Chagyr Formation in northwest Altaya, central Asia. We examined six topotypes lent to Dr V. A. Sytova by Dr V. A. Zheltonogova and these are referable to *Entelophyllum* and may well be conspecific with the European *E. fasciculatum*.

Entelophyllum sp. A

Text-fig. 4G–H

Material studied. RM Cn66046 from the Hamra Beds at Kättelviken 3, southern tip of Gotland.

Distribution. Gotland: late Ludfordian Stage.

Description. Small ceratoid corallite 20 mm tall and 11 mm in diameter immediately below the calice. With the proximal tip broken off, it does not indicate whether it is colonial or not.

Septa are radially arranged in two orders with 22 in each. Major septa are slightly withdrawn leaving an axial space 2 mm by 1 mm. Minor septa are one-half to three-fifths the length of the major. The septa of both orders are variable in the dissepimentarium, from slightly flexuose to straight. They are thickened and moderately cardinate in the cardinal quadrants only.

The longitudinal section is not median but indicates that the tabularium is a third to a half the diameter of the corallite wide and has a centrally raised area and probably a periaxial trough. The tabellae are globose and moderately spaced. The dissepiments are globose, up to 1 mm across, and not arranged in regular series.

Remarks. In growth form, size, septal number, open axial space, and longitudinal section, it resembles *E. fasciculatum* Wedekind, 1927, from the Eke Beds. It differs only in that the septa in the cardinal quadrants are thicker and more carinate than in *E. fasciculatum*.

Entelophyllum proliferum (Dybowski, 1874)

Text-fig. 4i–L

1874 *Cyathophyllum proliferum* Dybowski, p. 445, pl. 3, fig. 2, 2a, 2b.

non 1927 *Entelophyllum proliferum* (Dybowski); Wedekind, p. 23, pl. 29, figs 21–29, 33.

Lectotype. Chosen Wedekind (1927, p. 23), original of Dybowski, 1874, pl. 3, fig. 2 and 2a [non 2b]; EGM Col352, Slite Beds, Stora Karlsö, Gotland; late Sheinwoodian or early Homerian.

Material. Two specimens (Dybowski 1874, pl. 3, fig. 2, 2a, 2b) from Stora Karlsö and that of fig. 2b are only questionably assigned to this species as thin sections are not available.

Distribution. Gotland: late Sheinwoodian or early Homerian.

Diagnosis. Small bushy fasciculate corallum, increase peripheral parricidal; corallites up to 10 mm in diameter, major septa smooth, straight, number 20–22, leave an open axial space; minor septa weak; tabularium not distinctly biserial and periaxial trough not well developed; dissepiments variable in size, not regularly arranged.

Description. The lectotype is a small bushy corallum with a lower ceratoid to subcylindrical corallite producing five offsets one of which has a small bud in its calice. Budding in this mode is peripheral parricidal. The longitudinal thin section (Text-fig. 4i) suggests that the tabularium of the offset commenced as an extension of the periaxial trough of the parent and the neo-wall or part of it was inserted within the tabularium of the parent. The corallites vary from 8–9.5 mm in diameter before budding and the early corallite is 1.7 cm high and those of the second generation 1.2–1.3 cm. The epitheca is thin and shows very fine growth lines on slightly expanded growth bands. The second specimen figured by Dybowski is a tall tapering corallite 33 mm tall and

8 mm in diameter at the calice with four offsets developed in the calice. Dybowski's drawing shows concentric growth constrictions and low longitudinal ridges and furrows.

The septa are radially arranged, straight, thin and smooth. There are 20–22 major septa that extend three-quarters of the way to the axis leaving an open axial space almost 2 mm wide. Minor septa are weakly developed or discontinuous within the dissepimentarium.

The longitudinal section shows a well developed tabularium 0.6 the corallite diameter. In places it is not well delineated from the dissepimentarium. It consists of broad tabulae and supporting tabellae spanning the tabularium forming a raised flat axial area strongly downturned 1 mm from the tabularium boundary and then outturned to meet the dissepimentarium almost horizontally. There are twelve tabulae in 5 mm vertically. Dissepiments are highly variable in size and are irregularly arranged. They are globose with some three times the size of others. Some are horizontally based while others slope downward and inward.

Remarks. Dybowski (1874) gave the locality of his two specimens as Stora Karlsö on which is exposed the Slite Beds. In searching previous collections and in collecting from Stora Karlsö and other outcrops of the Slite Beds on Gotland, we have been unable to obtain further material. The possibility must be considered that Dybowski's specimens may not have come from Stora Karlsö. Of the Gotland species Dybowski's specimens of *E. proliferum* most closely resemble *E. fasciculatum* from the much higher upper Hemse and lower Eke Beds. Both forms have a wide axial area depleted of septa, a generally similar tabularium with a poorly defined periaxial trough, and a peripheral zone of irregularly distributed medium and large dissepiments. In the longitudinal section of *E. proliferum* the tabularium of the offset appears to originate as an extension of the periaxial trough of the parent (Text-fig. 4t), while in *E. fasciculatum* offsets originate from the dissepimental zone only. *E. proliferum* differs from *E. articulatum*, which also occurs in the Slite Beds, in having larger more irregular dissepiments and a tabularium that is much less well defined into two series.

Description and interpretation of this species are based on Dybowski's description and drawings, and photographs of the longitudinal section figured by Dybowski (1874, pl. 3, fig. 2a) and a transverse section on the same slide, kindly sent to us by Dr D. Kaljo. Wedekind (1927, p. 23) designated Dybowski's figures 2 and 2a as the lectotype, regarding the thin section 2a as being from part of 2. The thin longitudinal section is on the same slide as the transverse section but it is not known which specimen the transverse is from (D. Kaljo pers. comm. 1972). If the thin sections are from different specimens and are different from that figured as figure 2 by Dybowski, we select the longitudinal section as the primary type.

Entelophyllum dendroides sp. nov.

Text-fig. 5A–F

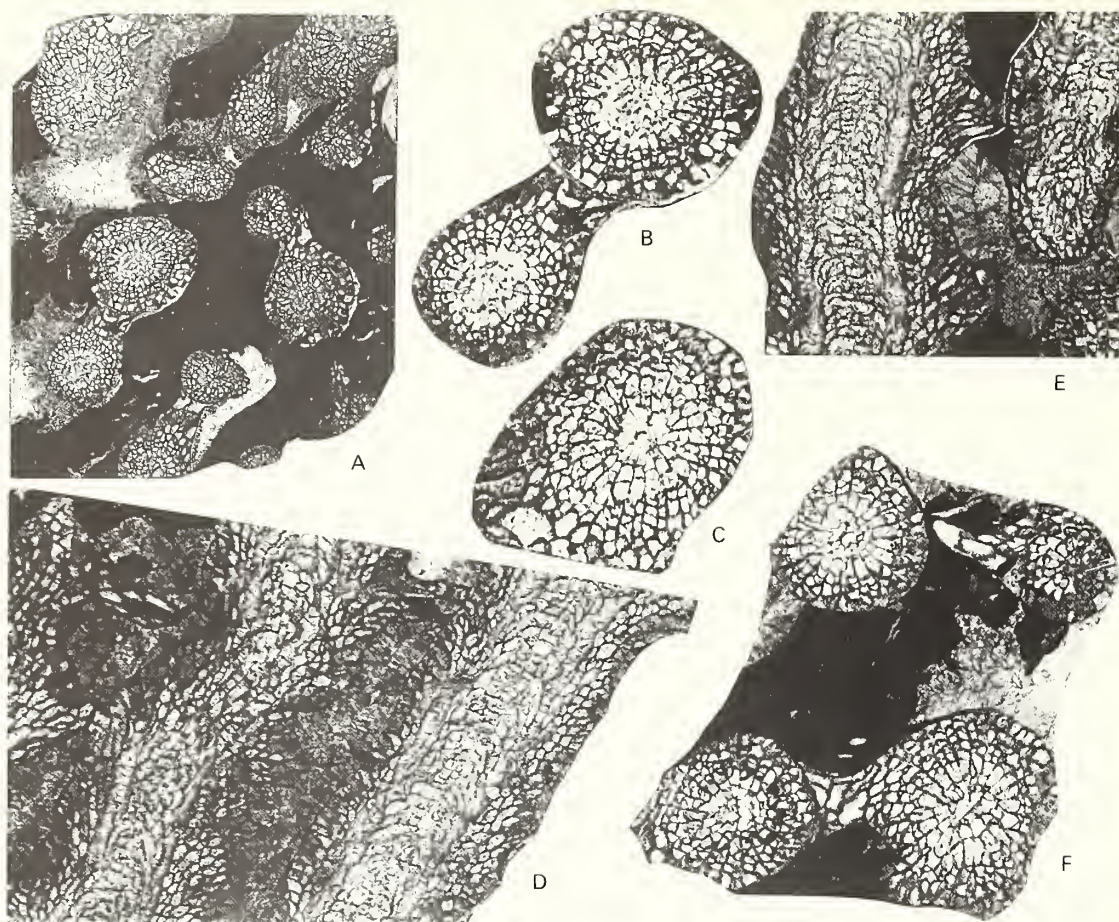
Holotype. RM Cn2560, Röda Lagret, Visby coast, Gotland; Telychian.

Material studied. Holotype (RM Cn2560, including two thin sections), and a paratype of four thin sections (RM Cn55554–Cn55557); both are given as from the Röda Lagret (probably from pebbles on the beach), Visby, west coast of Gotland (both figured).

Distribution. Gotland: Telychian.

Diagnosis. Dendroid colonies of closely-spaced small corallites 4–7 mm in diameter; septa typically straight, noncarinate; major septa number 20–23; 1 mm axial space into which some septa may extend; tabularium biserial with prominent periaxial trough; dissepiments small, globose; increase peripheral parricidal.

Description. The holotype is part of a dendroid colony and measures 30 × 40 mm in cross-section at its widest part and is 75 mm long. It is composed of small subcylindrical corallites 4–7 mm in diameter, typically separated by less than 5 mm. The corallites arise mainly in groups of four from the dissepimentarium of the parent by parricidal increase. They diverge rapidly outward soon after separation from each other and expand in diameter. They then tend to turn vertically and produce lateral extensions that abut adjacent corallites.



TEXT-FIG. 5. *Entelophyllum dendroides* sp. nov., Rôda Lagret, from pebbles on the beach at Visby, Gotland. A-D, RM Cn2560 (holotype); A-C, transverse sections, $\times 2$, $\times 4$, $\times 4$ respectively; D, longitudinal section, $\times 4$. E, RM Cn55555, longitudinal section, $\times 4$. F, RM C55556, transverse section, $\times 4$.

Budding across the colony appears irregular; one corallite is 30 mm tall before budding, another is in excess of 60 mm. Lateral expansions are not produced at the same level across the corallum.

The figured transverse section (Text-fig. 5F) shows the initial stages of increase where the neo-walls form as four scallops at the inner dissepimentarium, slightly expanding into the tabularium. A dissepiment is based on the neo-wall, and neo-septa project inwards from the dissepiment towards the atavo-septa. In the longitudinal section (text-fig. 5E) there is a suggestion of one offset being produced by nonparricidal increase but this cannot be definitely established.

Septa are typically long, radially arranged in two orders. The major septa number 20-23 in mature corallites and leave a narrow axial space (Text-fig. 5B and C). The septal ends are typically irregularly bunched near the axis in groups of two to three but two or more septa may extend irregularly to the axis. In immature corallites many of the major septa are confluent at the axis. Minor septa are half major septa in length and variously developed. They may be straight, slightly thinner than the major septa, projecting radially a short distance into the tabularium, and discontinuous.

Longitudinal sections are typically entelophylloid with the tabularium and dissepimentarium distinctly delineated and the tabularium separated into an axial and a periaxial series of tabellae (Text-fig. 5D). The tabularium is typically 0.6 the diameter of the corallite, and the axial series of tabellae 0.75 to 0.8 the diameter of the tabularium. The axial series consists of flat-topped tabellae that have steeply downturned edges and



TEXT-FIG. 6. *Entelophyllum pseudodianthus* (Weissmerl), Much Wenlock Limestone, Wenlock Edge, Shropshire; GSM 6575 (neoelectotype). A, longitudinal section, $\times 4$. B, transverse section, $\times 4$.

number 10–15 in 5 mm vertically. The periaxial series are flat or slightly concave upwards producing a pronounced periaxial trough with 20–22 tabellae in 5 mm vertically. The dissepiments are small, globose or slightly elongated and sloping downward and inward.

Remarks. This species is distinguished by its relatively small sized corallites and dendroid habit. It differs from the Llandovery *Petrozium dewari* Smith, 1930 and *P. losseni* (Dybowski 1874) by the more marked separation of the tabularium into axial and periaxial series and wider dissepimentarium.

Entelophyllum pseudodianthus (Weissmerl, 1894)

Text-figs 6A, B and 7A–E

- v1839 *Cyathophyllum dianthus* Goldfuss; Lonsdale, p. 690, pl. 16, figs 12b, 12c, 12d [non *Cyathophyllum dianthus* Goldfuss, 1826].
- 1894 *Cyathophyllum* (*Heliohyllum*) *pseudodianthus* Weissmerl, p. 591, pl. 47, figs 2 and 3.
- v1927 *Xylodes pseudodianthus* (Weissmerl); Lang and Smith, p. 475, pl. 35, fig. 9.
- v1929 *Xylodes pseudodianthus* (Weissmerl); Smith and Tremberth, p. 366, pl. 8, figs 3 and 4.

Neoelectotype. Here chosen, original of Lonsdale, 1839, pl. 26, fig. 12b, c, d; GSM 6575 and thin section PF 4617 from the Geological Society Collection, Much Wenlock Limestone, Wenlock Edge, Shropshire, England; Homerian.

Type material. Weissmermel (1894, p. 591) described *Cyathophyllum (Heliophyllum) pseudodianthus* as a new name for a species represented by the four specimens which had been figured as *Cyathophyllum dianthus* by Lonsdale (1839, pl. 16, fig. 12, 12a–e). Lang and Smith (1927, p. 473) stated that one of Lonsdale's four specimens (fig. 12e) is lost and that the other three represent three distinct species, each belonging to a different genus. They state that only Lonsdale's figures 12b–d (all from the one specimen: GSM 6575) represents the species described by Weissmermel as *C. (H.) pseudodianthus* and selected as lectotype the specimen figured by Weissmermel (1894, pl. 47, fig. 3) from a boulder in the glacial drift of Lauth, Germany. That specimen, in the East Prussian Provincial Museum at Königsberg (now Kaliningrad), was never sectioned and was destroyed during the Second World War (Dr V. A. Sytova pers. comm.).

We have thus selected one of Weissmermel's original syntypes as the neoelectotype, the specimen figured by Lonsdale (1839, p. 16, fig. 12b–d); GSM 6575, and herein refigured (Text-figs 6A, B and 7E).

Material studied. Neoelectotype (GSM 6575) and twenty-four specimens from the collections of the GSM, BMNH, UO, SM, UB, and UQ from the Much Wenlock Limestone, Wenlock Edge, Shropshire; figured: GSM 6575 (neoelectotype), BMNH R2022. Farley Member, Coalbrookdale Formation; Much Wenlock Limestone of Dudley, Worcestershire, including Wren's Nest (numerous specimens from same collections as the Wenlock Edge material above; figured: UB 124); Much Wenlock Limestone of May Hill, Gloucestershire (figured BU 8715); and lower Elton Beds, from Ledbury Quarry, Malvern, Herefordshire.

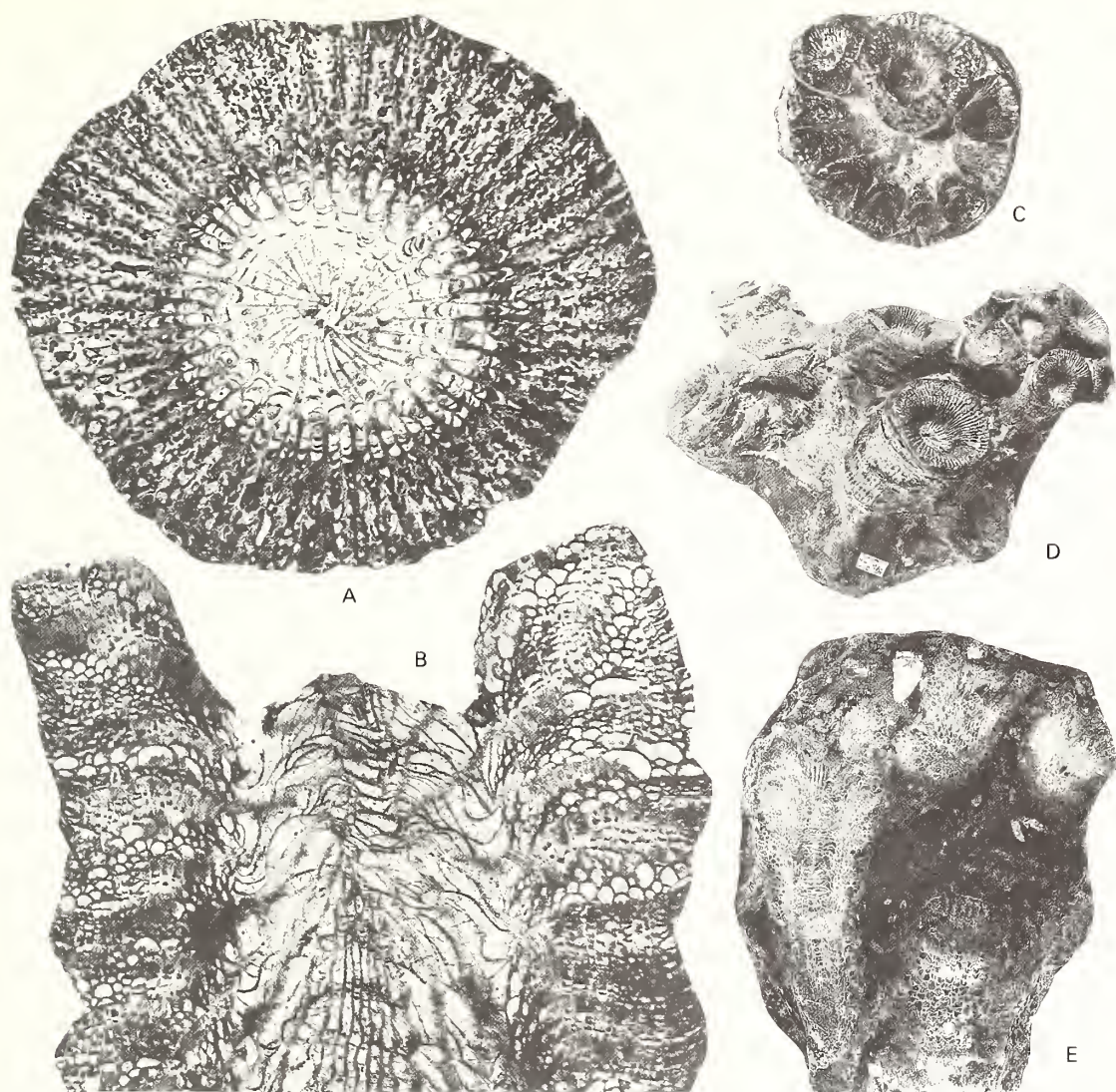
Distribution. England: Homerian to early Gorstian; Estonia: Ludlow to ?Pridoli; Poland: ?early Pridoli.

Diagnosis. Typically small bushy coralla of turbinate to rapidly expanding subcylindrical corallites up to 25 mm in diameter; increase peripheral parricidal with up to 10 offsets. Septa 20–33 in each order, long, thickened in dissepimentarium and heavily carinate to aerolate; major septa slightly withdrawn from axis; minor septa rarely contratigent. Tabularium biserial with periaxial trough; dissepiments globose, horizontally based at periphery and steeply inclined axially.

Description. The coralla are small and bushy, up to 200 mm in diameter and 150–200 mm in height, consisting of two to five generations of corallites (Text-fig. 7D). The coralla are fasciculate, generally formed of rapidly expanding corallites 60 mm in height and 15–20 mm in diameter but in some coralla they may be cylindrical and up to 100 mm in height. The neoelectotype is a small bushy clump 20 mm in diameter and 40 mm high, consisting of 8–10 corallites (Text-fig. 7E). Budding is peripheral, parricidal with up to ten corallites originating at the extreme margin of the calyx. Corallites rapidly expand and quickly diverge giving the corallum a radiating appearance (Text-fig. 7D); they have strong contractions and expansions but few connecting processes. Corallite walls are thin and epithecate.

Major septa number 21–33 (mean 27 at diameter 12 mm) in adult stages (Text-fig. 6B). Some major septa extend to the axis while others are withdrawn leaving an axial space up to 3 mm in diameter. Axial ends are commonly turned aside or twisted. Minor septa typically do not project into the tabularium, are commonly 0.6–0.7 the length of the major, and are only rarely contratigent. In the dissepimentarium both orders of septa are thickened, heavily carinate and commonly aerolate, but in parts of some corallites they are relatively smooth. Carinae are zigzag and parallel the trabeculae. In the outer dissepimentarium they diverge at a small angle to the vertical and are fanned over the inner dissepimentarium so that at the dissepimentarium/tabularium boundary they are 30° to the horizontal.

In longitudinal section the dissepimentarium and tabularium are distinctly delineated. The tabularium is 6–7 mm wide and differentiated into two series of tabellae. In forms with septa extending to the axis the axial series are domed and relatively high (Text-fig. 6A), while in those with the septa withdrawn from the axis they are flat or sagging and of low profile (Text-fig. 7B). A narrow series of small, flat or slightly saucered tabellae span the area between the axial series and the dissepimentarium forming a periaxial trough. Dissepiments are small, globose, occurring in almost horizontal rows at the periphery and steeply inclined inwards and downwards at the tabularium boundary. In some specimens broad zones of more globose dissepiments alternate vertically with thinner zones of smaller and slightly thicker dissepiments (Text-fig. 7B). The former correspond to expansions of the corallite diameter and the latter to the contractions.



TEXT-FIG. 7. *Entelophyllum pseudodanthus* (Weissmer). A and B, BU 8715, Much Wenlock Limestone, May Hill, Gloucestershire; A, transverse section showing typical carinate and thickened septa, $\times 4$. C and D, Much Wenlock (Dudley) Limestone, Dudley, Worcestershire; C, UB 124, calical view showing peripheral parricidal increase, $\times 1$; D, UO C17516, oblique view showing typical loose fasciculate corallum, $\times 1$. E, GSM 6575 (neoelectotype), Much Wenlock Limestone, Wenlock Edge, Shropshire, polished surface, $\times 2$.

Remarks. In England, *Entelophyllum articulatum anglicum* and *E. pseudodanthus* have the same distribution and commonly occur together. We have included those forms with their septa typically thickened, highly carinate and in some cases aerolate in *E. pseudodanthus*, as did Smith and Tremberth (1929). These specimens generally have squatter coralla, more turbinatate corallites, shorter minor septa that are rarely contratigent, and less regular biserial tabularia. However, some have corallites that are slender and cylindrical, minor septa that project into the tabularium and are contratigent, and have regular biserial tabularia. On the other hand corallites in some colonies

referred to *E. articulatum anglicum* are turbinate or have some thickened and carinate septa. Thus some specimens seem to be gradational between the two forms and their specific designation is arbitrary.

Entelophyllum pseudodianthus transiens (Prantl, 1940)

Plate 6, figs 5–7

1940 *Xylodes pseudodianthus transiens* Prantl, p. 13, pl. 1, fig. 4; pl. 3, figs 1, 2, 4.

Holotype. Prantl, 1940, pl. 1, fig. 4, from the Kopanina Formation, 'Amerika' quarries near Morina (Budnany of Prantl 1940), Czechoslovakia; Gorstian.

Material. Interpretation based on photographs of thin sections figured by Prantl (1940, pl. 3, figs 1, 2, 4).

Distribution. Bohemia: ?late Homeric to ?Gorstian.

Diagnosis. Small bushy coralla with ceratoid to subcylindrical corallites 11–17 mm in diameter; increase peripheral, parricidal. Major septa 31–34, withdrawn up to 1 mm from axis, cardinal septum projecting into axial space; septa thin in tabularium; continuous, some thickened and carinate in dissepimentarium. Tabularium distinctly biserial with axial tabellae flat topped; dissepiments small, globose, inclined axially.

Remarks. Prantl (1940) proposed this species for forms that show both long thin smooth septa typical of *E. articulatum* and thickened carinate septa typical of *E. pseudodianthus*. Considering the variation in *E. articulatum anglicum* and *E. pseudodianthus* described previously, the Bohemian form could well belong to this series. The lack of heavily carinate and cavernous septa suggest similarities to *E. articulatum anglicum* rather than *E. pseudodianthus*. In size and septal number, it is more like specimens of the subspecies from the Elton Beds of similar age.

Entelophyllum prosperum (Počta, 1902)

Plate 6, figs 1–4

1902 *Cyathophyllum prosperum* Počta, p. 105, pl. 43, figs 1, 2, 10–19, 23–29, 36–41; pl. 44, figs 1–33; pl. 45, figs 1–5, 18–39; pl. 46, figs 8–24; pl. 103, figs 6–8; pl. 109, fig. 8.

1902 *Cyathophyllum minusculum* Počta, p. 104, pl. 42, figs 1–8.

1940 *Xylodes prosperus prosperus* (Počta); Prantl, p. 8, pl. 1, figs 5 and 6; pl. 2, figs 2, 5, 7.

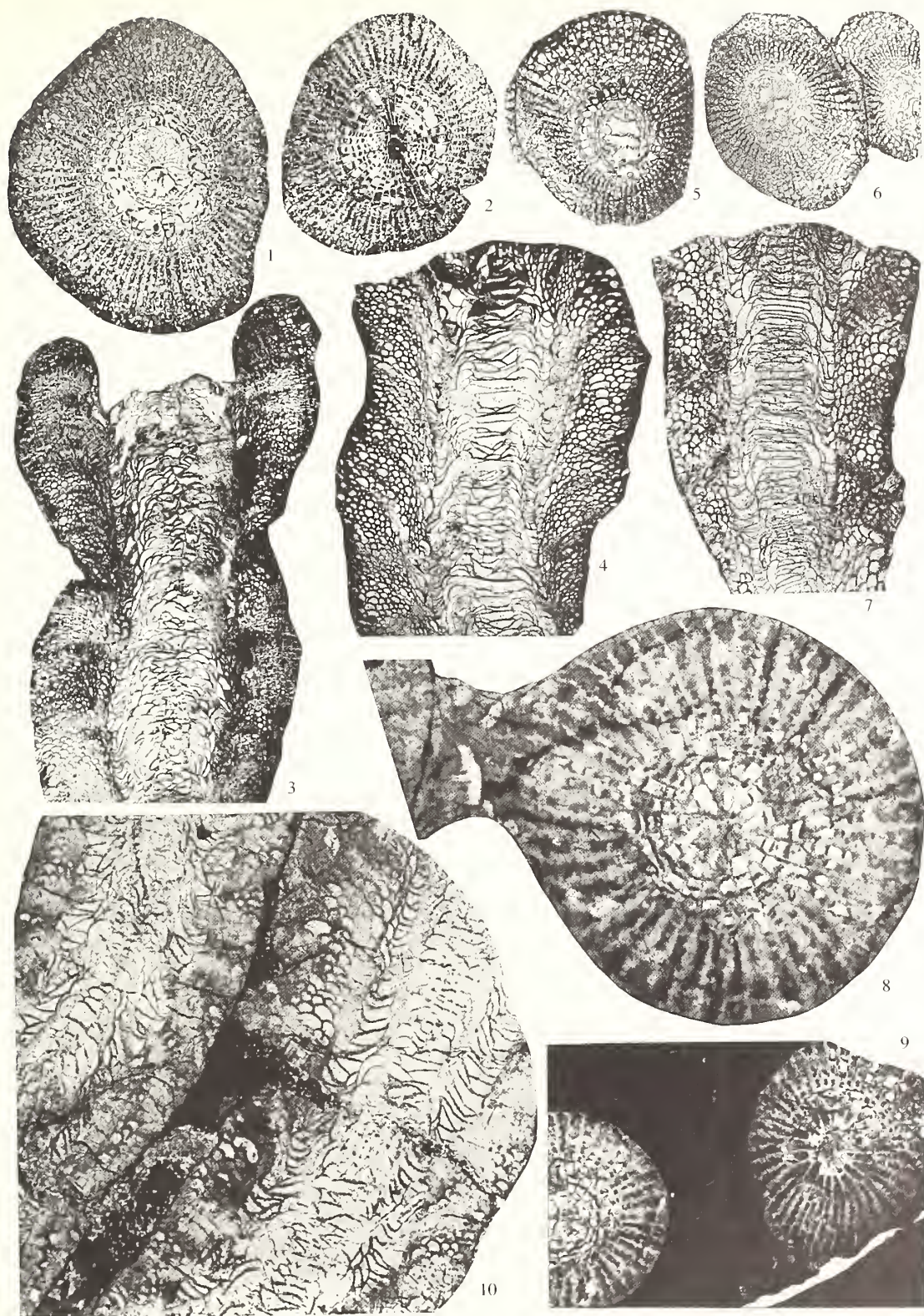
Lectotype. Chosen Prantl (1940, p. 8), original of Počta, 1902, pl. 44, figs 1–4 from Budnaner Kalksteine, Kopanina Formation at Tachlovice, Czechoslovakia; Gorstian.

EXPLANATION OF PLATE 6

Figs 1–4. *Entelophyllum prosperum* (Počta), Kopanina Formation, Tachlovice, Czechoslovakia. 1, NM No. 768, original of Počta (1902, pl. 103, fig. 7), transverse section, $\times 2$. 2, NM unnumbered, original of Prantl (1940, pl. 2, fig. 2), transverse section $\times 2$. 3, NM No. 855, original of Počta (1902, pl. 103, fig. 8), longitudinal section, $\times 2$. 4, NM No. 473, original of Počta (1903, pl. 103, fig. 6), longitudinal section, $\times 2$.

Figs 5–7. *Entelophyllum pseudodianthus transiens* (Prantl), Kopanina Formation, 'Amerika' quarries, near Morina, Czechoslovakia. 5, NM 26329, original of Prantl (1940, pl. 3, fig. 2), transverse section, $\times 2$. 6, NM 26329, original of Prantl (1940, pl. 3, fig. 4), transverse section, $\times 2$. 7, NM 26329, original of Prantl (1940, pl. 3, fig. 1), longitudinal section, $\times 2$.

Figs 8–10. *Entelophyllum confusum* (Počta), Upper Litén Group [Motol Formation], 'V Kozle' between Beroun and Srbsko, Czechoslovakia. 8 and 9, NM unnumbered, transverse sections, $\times 7.5$, $\times 4$, respectively. 10, NM unnumbered, longitudinal section, $\times 4$.



Material. Interpretation based on photographs of thin sections figured by Počta (1902, pl. 103, figs 6–8) and Prantl (1940, pl. 2, fig. 2); all from Kopanina Formation at Tachlovice.

Distribution. Bohemia: Gorstian.

Diagnosis. Small bushy coralla with trochoid to subcylindrical corallites 18–19 mm, maximum 35 mm, in diameter; increase peripheral parricidal. Major septa 28–40, withdrawn from axis in the cardinal quadrants leaving axial space elongate in counter-cardinal plane; minor septa 0.6 the length of major; septa considerably thickened, heavily carinate to aerolate, continuous in dissepimentarium. Tabularium biserial; axial series varying from small tabellae forming high domes to large complete tabellae slightly sagged axially; dissepiments small, globose, horizontally based at periphery and steeply inclined axially.

Remarks. Prantl (1940) in redescribing the entelophylloid corals in the collection of Počta (1902), recognized two subspecies for the material described as *Cyathophyllum prosperum* and the synonymy given above is that of the nominate subspecies. *E. prosperum* is characterized by thickened and heavily carinate septa with the outer dissepimentarium appearing reticulate in transverse section and resembling *E. pseudodianthus* from Britain. These two species are very similar, the Bohemian species only differing in its slightly greater size and more numerous septa, and the more noticeable fossula. Offsets arising right at the margin of the parent in the specimen figured by Prantl (1940, pl. 1, fig. 6) are identical to that figured herein for *E. pseudodianthus* (Text-fig. 7c). The Bohemian form might best be considered a subspecies of *E. pseudodianthus*. However, not enough material is available to us and the type locality 'Tachlovice' is today unknown but thought to have been in a mine (A. Galle, pers. comm.).

Entelophyllum prosperum crassum (Prantl, 1940)

- 1902 *Cyathophyllum prosperum* Počta, p. 105, pl. 43, figs 3–9, 20–22, 30–35; pl. 44, figs 34–40; pl. 45, figs 40–42; pl. 46, figs 1–7.
1940 *Xylodes prosperus crassus* Prantl, p. 11, pl. 1, figs 7–9; pl. 2, fig. 6; pl. 3, fig. 3.

Holotype. Počta, 1902, pl. 44, figs 33–34, from Budnaner Kalksteine, Kopanina Formation at Tachlovice, Czechoslovakia; Gorstian.

Material. No material was available for this study.

Distribution. Bohemia: Gorstian.

Remarks. This subspecies was described by Prantl (1940) for the larger specimens of *E. prosperum* from the same strata. The originals of Prantl (1940, pl. 2, fig. 6; pl. 3, fig. 3) have not been located.

Entelophyllum confusum (Počta, 1902)

Plate 6, figs 8–10

- 1902 *Cyathophyllum confusum* Počta, p. 103, pl. 99, figs 3–11.
1940 *Xylodes confusus* (Počta); Prantl, p. 16, pl. 3, figs 5 and 6.
1981 *Carinophyllum confusum* (Počta); Hill, fig. 127, 2d, e.

Lectotype. Chosen Prantl (1940, p. 16), original of Počta, 1902, pl. 99, fig. 3, from the Budnaner Kalksteine, Kopanina Formation of Tachlovice, Czechoslovakia; Gorstian.

Material. Interpretation based on photographs of the thin sections figured by Prantl (1940, pl. 3, figs 5 and 6) from the upper Liten Group (Motol Formation), 'V Kozle' between Beroun and Srbsko (Homerian). Fedorowski and Gorianov (1973) referred three specimens of the Eichwald collection from Estonia to this

species, one from the Gorstian-Ludfordian Paadla Horizon of Pilguse and two from the late Ludfordian Kuressaare Horizon of Lode.

Distribution. Bohemia: Homeric and Gorstian; Estonia: Ludlow.

Diagnosis. Small dendroid to phaceloid coralla; corallites cylindrical, 8–14 mm in diameter; increase peripheral paricidal. Septa fusiform, carinate in dissepimentarium; 22–24 major septa extend almost to axis leaving small axial space; cardinal septum projects slightly into axial space. Tabularium biserial; axial series high, flat topped; dissepimental zone broadly arched; dissepiments small, globose.

Remarks. This species is distinguished by the fusiform and carinate nature of septa, characters Strelnikov (1964, p. 59) used to typify his new genus *Carinophyllum* with *E. confusum* as type species. These features and the corallite size seem to distinguish the Bohemian material as a distinct species but we do not consider the carination and thickening to be of generic significance.

Entelophyllum lauense sp. nov.

Plate 7, figs 1–12

Holotype. RM Cn66047, *Rhizophyllum* limestone, lower Eke Beds, Lau Backar 1, southeast Gotland; middle Ludfordian.

Material studied. *E. lauense* is known only from the type locality (ten specimens; figured: RM Cn66047 (holotype); UQ F35165, 35169, 35170, 35281 (paratypes)).

Distribution. Gotland: middle Ludfordian.

Diagnosis. Presumably fasciculate, corallites flaring after early trochoid stage, up to 25 mm in diameter and 20 mm high; major septa 30–32, cardinal fossula confluent with axial space; minor septa 0.6–0.7 length of major; septa in dissepimentarium thickened axially and heavily carinate to retiform peripherally. Tabularium biserial with axial tabellae domed typically with axial sag; dissepiments small globose; broad dissepimentarium zone peripherally domed.

Description. Broken isolated corallites are trochoid initially but flare rapidly producing wide, everted calices 14–25 mm in diameter, while the corallites are less than 20 mm high. The dissepimental zone forms a broad calical platform that may show several rejuvenescences. They surround moderately deep tabularial pits that have a shallow trough about the outside and a central depression which may be connected to the trough by a depressed cardinal fossula (Pl. 7, fig. 3). Early stages of several specimens show either broken early tips or crescent-shaped broken walls that are interpreted as fragments from a parent corallite. Some corallites show a supporting buttress (Pl. 7, fig. 4). One specimen, UQ F35165, shows two generations of budding with one offset arising at a rejuvenescence by peripheral non-paricidal budding and the parent has two small offsets developing in the dissepimentarium 8 mm higher. The holotype has at least three offsets beginning by the development of scalloped neo-walls near the inner margin of the dissepimentarium (Pl. 7, fig. 1).

There are 30–32 major septa arranged pinnately about a long cardinal septum which bisects a distinct fossula (Pl. 7, fig. 11). They are slightly withdrawn abaxially leaving a narrow axial space 1–2 mm in diameter, into which the cardinal fossula opens. The septa in the tabularium are thin, straight or slightly flexuose at their axial extremities. The minor septa are well developed only slightly thinner than the major and 0.6–0.7 their length, projecting a short distance into the tabularium. In the dissepimentarium both orders are variably thickened, zigzag, irregularly carinate to retiform. The thickening is more pronounced in the inner dissepimentarium and the carination increases toward the periphery. Carinae typically alternate, arising from the angles of the zigzag septa but in places they are so numerous and the segments of the septa so short and turned away from the plane of the septum that the carinae appear opposite each other.

The tabularium expands rapidly with growth and is 0.6–0.7 the diameter of the corallite immediately below the calice. The tabularial floors are domed centrally with a slight axial depression, and downturned in the outer tabularium producing a periaxial trough (Pl. 7, fig. 2). The axial tabellae are relatively large and globose, and their downturned edges rest on tabellae below or outturn to the dissepimentarium. Periaxial tabellae are flat or concave upwards. Dissepiments are small, globose, peripherally domed, and not arranged in vertical series.

Septa appear to be composed of a uniserial row of monacanthine trabeculae 0.01–0.02 mm in diameter. Extension of the fibres of the trabeculae form the carinae. Both the trabeculae and carinae show a fanning over the dissepimentaral floor, becoming flatter near the dissepimentarium/tabularium boundary and then becoming steep again axially.

Remarks. All specimens are isolated but they are interpreted as being broken offsets from loosely fasciculate colonies. The colonial nature is also suggested by UQ F35165 which shows two generations of budding.

E. lauense differs from other described Gotland species of *Entelophyllum* by its corallum form, flat flaring nature of the corallites, and heavy carination and thickening of the septa. In the latter regard, it resembles *E. pseudodiantus* but differs from it in that the corallites are much flatter and have well developed fossulae.

There is some reservation in referring *E. lauense* to *Entelophyllum* because it is not clearly as fasciculate, the cardinal septum and fossulae are more pronounced, and the septa more heavily carinate than in the type species. However, as discussed above, it appears to be compound with at least two generations of buds. The development of the cardinal septum is variable in other species of *Entelophyllum* and this is not regarded as a generic character. The carination and retiform nature of the septa are comparable with that of *E. pseudodiantus* and *E. prosperum* which we included in *Entelophyllum* rather than separating out the carinate forms as *Stereoxylodes* Wang, 1944. There are similarities to *Nanshanophyllum typicum* Yu, 1956, a solitary form, heavily carinate in the dissepimentarium, showing a cardinal fossula opening into an axial space. Pedder (1976) considered *Nanshanophyllum* Yu to be a subgenus of *Stereoxylodes*.

Entelophyllum hamraense sp. nov.

Plate 8, figs 1–9

Holotype. RM Cn66048; Hamra Beds, Nårs fyr 1, southeast Gotland; late Ludfordian.

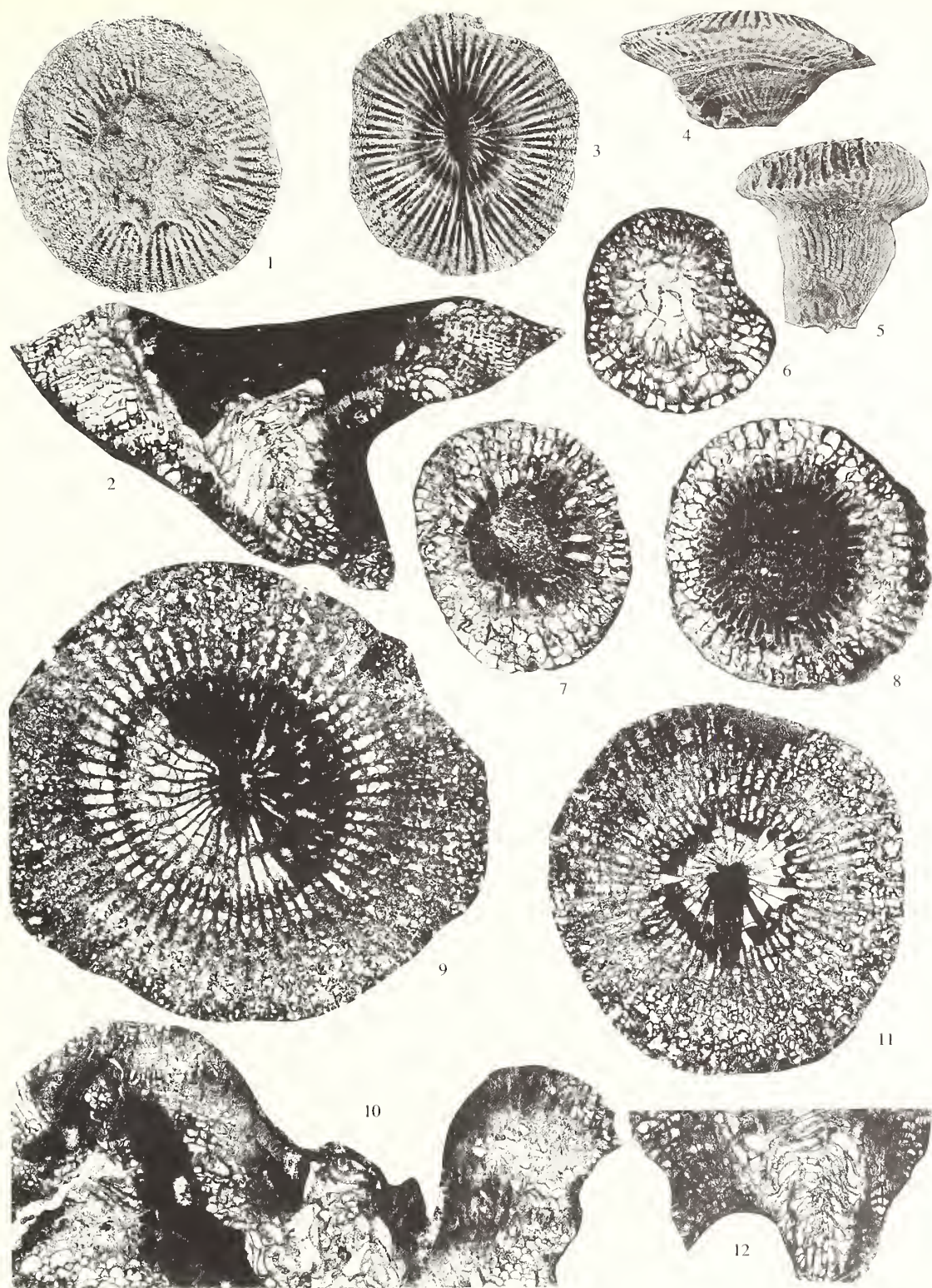
Material studied. Hamra Beds of Gotland: the type locality (one specimen; figured: RM Cn66048 – holotype); Kättelviken 3, southern tip of Gotland (one specimen; figured: UO 10672); Hoburgen 2, southern tip of Gotland (six specimens; figured: UQ F34001); ?Hamra or Lower Sundre Beds at Juves 3, southern tip of Gotland (one specimen; figured: RM Cn66049).

Distribution. Gotland: late Ludfordian.

Diagnosis. Fasciculate corallites trochoid to ceratoid, maximum diameter 25 mm, height 40 mm, peripheral parricidal increase. Major septa number 27–31, withdrawn from axis, axial ends slightly thickened, septal segments and long cardinal septum common in axial space; minor septa commonly contratigent; septa heavily carinate and thickened in inner dissepimentarium; tabularium regularly biserial; dissepimentarium broad, dissepiments small, globose.

EXPLANATION OF PLATE 7

Figs 1–12. *Entelophyllum lauense* sp. nov., *Rhizophyllum* limestone, Eke Beds, Lau Backar 1, 1.0 km NE of Lau, southeast Gotland. 1 and 2, RM Cn66047 (holotype); 1, calical view showing incipient buds, $\times 2$; 2, longitudinal section, $\times 4$. 3 and 4, UQ F35170; 3, calical view, $\times 2$; 4, lateral view, $\times 2$. 5–8, UQ F35281; 5, lateral view, $\times 2$; 6, transverse section from base, $\times 4$; 7, transverse section from central part, $\times 4$; 8, transverse section of calice, $\times 4$. 9 and 10, UQ F35165; 9, transverse section, $\times 4$; 10, longitudinal section showing edge of second corallite, $\times 4$. 11 and 12, UQ F35169; 11, transverse section $\times 4$; 12, longitudinal section, $\times 4$.



Description. Corallites are trochoid to ceratoid commonly occurring as isolated broken offsets up to 25 mm in diameter and 40 mm in height. The holotype consists of three offsets, 18, 18 and 20 mm in diameter and 35 mm in height, arising from the weathered edge of a calice. One of the offsets has at least three offsets in its calice. Another specimen, UO 10672, shows three small trochoid corallites arising from the periphery of a corallite 17 mm in diameter. Increase is peripheral parricidal.

Major septa number 27–30 and are smooth and straight in the tabularium, commonly withdrawn from the axis leaving an axial space 2–4 mm in diameter (Pl. 8, fig. 6). The cardinal septum and rarely the counter are longer than the others and project well into the axial space. Axial ends of septa are commonly thickened and discrete septal segments are common in the axial space based on the axial tabellae. Minor septa are 0.5–0.75 the length of the major and are commonly contratingent. In the dissepimentarium they are commonly as thick as the major and both are dilated in the inner parts and strongly carinate in the outer parts (Pl. 8, fig. 4). Carinae on the thickened inner parts are short and stout, and in places appear to have short prickles coming off them as though they were extensions of secondary trabeculae. In the outer parts the carinae are longer and more numerous, coming off the angles of the zigzags of the septa. The long carinae give a rather ragged appearance to the septa and only rarely are they retiform or aerolate.

The tabularium is 0.4–0.5 the diameter of the corallite, domed centrally with the tabulae sloping steeply downward peripherally and then turning outwards giving a shallow periaxial trough (Pl. 8, figs 5 and 7). The central area is composed of numerous globose tabellae. In places where the outer globose tabellae do not reach the dissepimentarium, flat periaxial tabellae span the space. Dissepiments are small, globose, not arranged in vertical series, and commonly flat peripherally but inclined axially downward near the tabularium.

Remarks. Specimens from Hoburgen are mainly isolated corallites but have similar internal structures to the holotype. Some may be initial protocorallites while others may be offsets broken from loosely fasciculate colonies.

E. hamraense differs from *E. lauense* from the Eke Beds, which also is heavily carinate, in that the corallites are taller, no fossula is developed, the septa are thicker in the inner dissepimentarium, and the septal ends commonly extend into the axial area. The occurrence of short prickles on the carinae suggests that the trabeculae may bear secondary trabeculae, which is not an entelophylloid character.

This species differs from *E. pseudodianthus* in that its axial space is not as open, the axial ends of the septa are not grouped as in the latter species and there is not as regular a biserial tabularium.

Entelophyllum? visbyense Wedekind, 1927

Plate 9, figs 1–9

v*1927 *Entelophyllum visbyense* Wedekind, 1927, p. 24, pl. 7, figs 9 and 10.

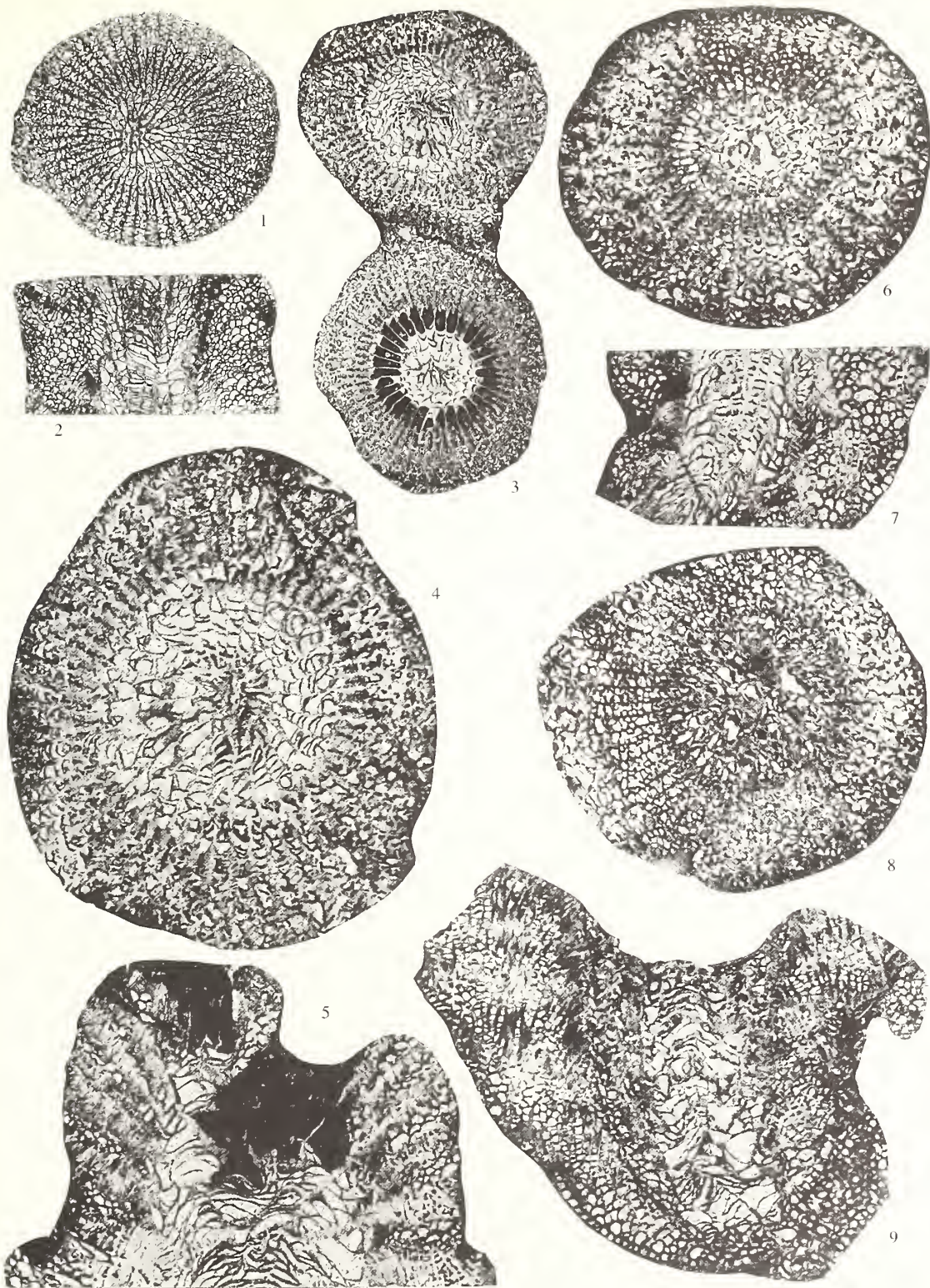
v*1927 *Entelophyllum anschutzi* Wedekind, 1927, p. 24, pl. 7, figs 7 and 8.

Holotype. Wedekind, 1927, pl. 7, figs 9 and 10; RM Cn54873, Högklint Beds, Gutevågen 3 [= Cement factory], Visby, Gotland; Sheinwoodian.

Material studied. Four specimens from the type locality; figured: RM Cn54873 (holotype), SMF Wdkd. 10308–10309 (holotype of *E. anschutzi*), RM Cn66196, Cn66197. Neuman and Hanken (1979) recorded this

EXPLANATION OF PLATE 8

Figs 1–9. *Entelophyllum hamraense* sp. nov. 1 and 2, UQ F34001, upper Hamra Beds, Hoburgen 2, southern tip of Gotland; 1, transverse section, $\times 2$; 2, longitudinal section, $\times 2$. 3–5, RM Cn66048 (holotype), lower Hamra Beds, Nårs fyr 1, coast at När, southeast Gotland; 3 and 4, transverse sections, $\times 2$, $\times 4$, respectively; 5, longitudinal section, $\times 4$. 6 and 7, OU 10672, Hamra Beds, Kättelviken 3, coast below road, 3.5 km N of Hoburgen, southern tip of Gotland; 6, transverse section, $\times 4$; 7, longitudinal section, $\times 4$. 8 and 9, RM Cn66049, Sunde Beds, Juvés 3, western side of road at Juvés, 2 km E of Hoburgen, southern tip of Gotland; 8, transverse section, $\times 4$; 9, longitudinal section, $\times 4$.



species from the Upper Visby and lowermost Högklint Beds in the Vattenfallsprofilen 1, near the ferry harbour of Visby.

Distribution. Gotland: Sheinwoodian.

Diagnosis. Phaceloid, corallites 10–12 mm in diameter, closely spaced, increase parricidal; major septa number 20–23, straight, thickened in inner tabularium, withdrawn from the axis leaving a broad axial space; minor septa very short; tabularium broad, axial tabulae flat-topped or sagging, weakly developed axial trough; dissepimentarium irregularly narrow, in one to four vertical series.

Description. The holotype is of a subcylindrical corallite 11 mm in diameter. Other specimens are fragments of large phaceloid coralla consisting of closely packed cylindrical corallites 10–12 mm in diameter, some are crushed due to later compaction. Calices are moderately deep with inverted conical sides and a wide flat axial floor. Increase is parricidal (Pl. 9, figs 8 and 9) with up to 12 offsets originating in the one calice. The neo-wall is initiated in the tabularium and it appears as though part of the tabularium of the parent is continuous with that of the offset.

In transverse section major septa are prominent, thickened in the outer tabularium and taper axially and some peripherally (Pl. 9, fig. 4). They are 0.6–0.8 the radius of the corallite in length and number 20–23 in mature corallites. In some the cardinal septum is shortened and may lie in a shallow fossula. The counter and counterlateral septa may be slightly extended. In the dissepimentarium major septa become irregular in places with the stereome that thickened them in the tabularium continuous onto the dissepiments. They may be thickened into triangular bases at the wall. Minor septa are short, 0.2–0.3 the length of the major, much thinner than the major, and in places interrupted by interseptal dissepiments.

The tabularium is 0.65–0.75 the diameter of the corallite in width, composed of tabulae that are flat or axially sagged with the edges downturned initially, then turned outward to meet the dissepimentarium nearly horizontally (Pl. 9, fig. 7). There are 8–15 tabulae in 5 mm vertically. Dissepiments are irregular in size and vary from small globose forms to more elongate ones, arranged in one to four rows (Pl. 9, fig. 8), three and rarely four in the holotype (Pl. 9, fig. 2).

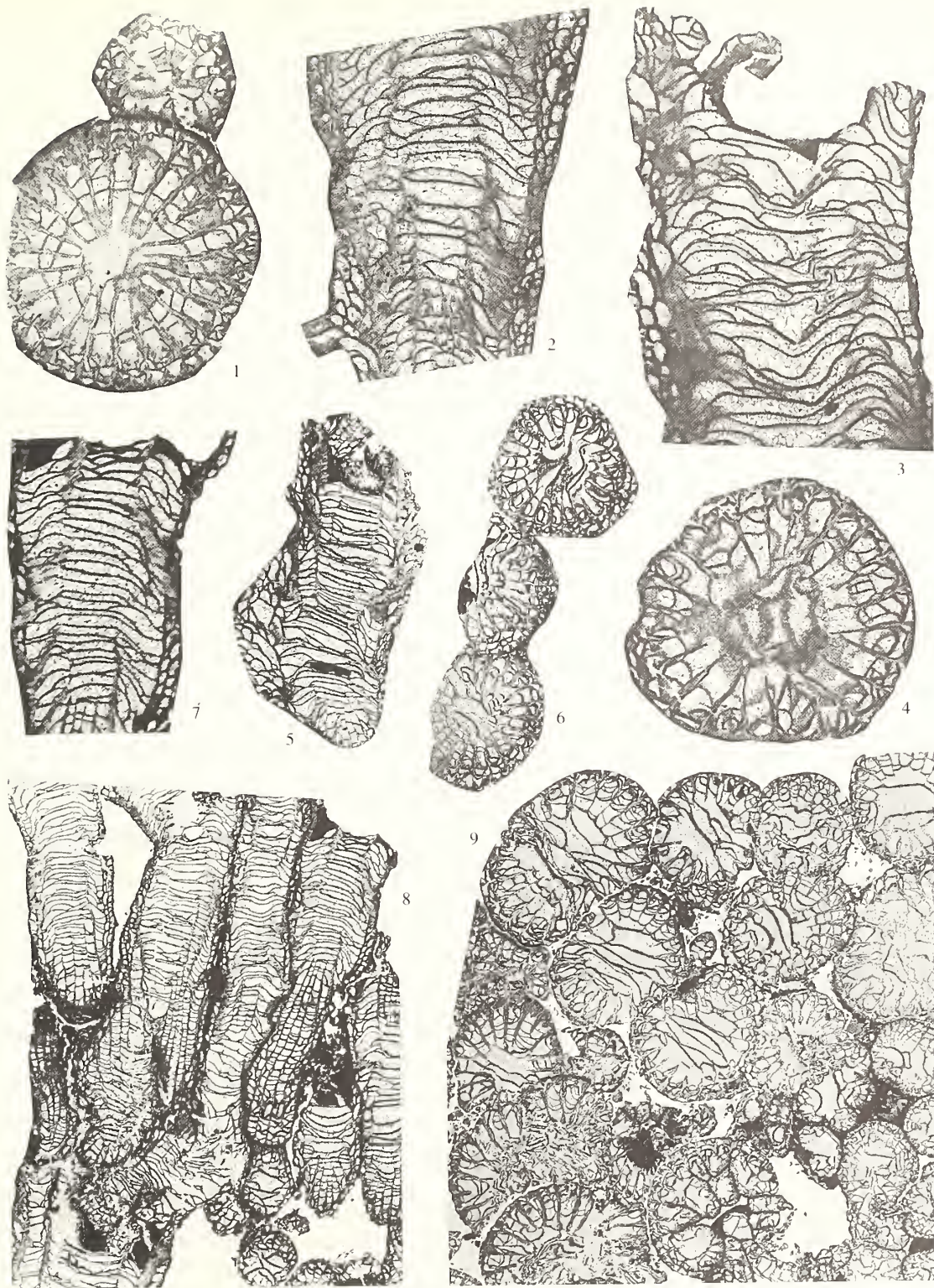
Septa are recrystallized in the holotype but appear to be monacanthate, with the monacanth sloping in and upward toward the axis at about 45° peripherally, and steepening axially to 55°–60°. There are approximately 3 trabeculae per 0.4 mm in vertical section.

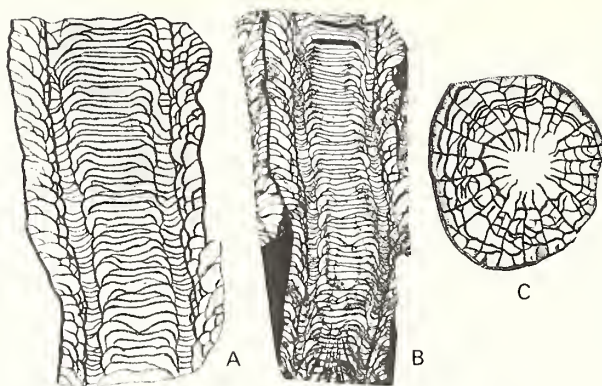
Remarks. We consider *E.?* *visbyense* to belong to some genus other than *Entelophyllum* because of the striking differences in character in both transverse and longitudinal section when compared to *E. articulatum*. The tabularium is not distinctly divided into two series with a well developed periaxial trough, and the septa are much more thickened and more typically withdrawn from the axis. The material at hand, however, is not considered adequate as a basis for defining a new genus.

The holotypes of *E.?* *visbyense* and *E.?* *anschutzzi*, both from the same locality and described by Wedekind (1927), show only minor differences. In transverse section *E.?* *anschutzzi* has thinner major septa that are more withdrawn from the axis, leaving a broader axial space, and in longitudinal section the tabularium sags compared with more flat tabulae in *E.?* *visbyense*. Sections through many corallites of the one corallum show similar variations (Pl. 9, figs 8 and 9). For these reasons, we are treating them as conspecific as did Neuman and Hanken (1979, p. 89).

EXPLANATION OF PLATE 9

Figs 1–9. *Entelophyllum?* *visbyense* Wedekind, Högklint Beds, Gutevägen 3, 1.54 km SW of Visby Cathedral, Gotland. 1 and 2, RM Cn54873 (holotype), original of Wedekind (1927, pl. 7, fig. 10); 1, transverse section, $\times 4$; 2, longitudinal section, $\times 4$. 3 and 4, from holotype of *E. anschutzzi* Wedekind, (1927, pl. 7, figs 7 and 8); 3, SMF Wdkd. 10308, longitudinal section, $\times 4$; 4, SM Wdkd. 10309, transverse section, $\times 4$. 5 and 6, RM Cn66196; 5, longitudinal section, $\times 2$; 6, transverse section, $\times 2$. 7–9, RM Cn66197; 7 and 8, longitudinal sections, $\times 4$, $\times 2$, respectively; 9, transverse section showing parricidal increase, $\times 2$.





TEXT-FIG. 8. *Entelophyllum? dalecarlicum* (Lindström), RM Cn57149 (holotype), Styggforsen Limestone, Styggforsen, Siljan district, Dalecarlia, central Sweden. A, reproduction of Lindström (1880, pl. 2, fig. 8), $\times 3$. B, thin section from which Lindström's figure was drawn, showing accuracy of the drawing, $\times 2$. C, reproduction of Lindström (1880, pl. 1, fig. 22), $\times 3$.

Entelophyllum? dalecarlicum (Lindström, 1880)

Text-fig. 8A–C

1880 *Cyathophyllum dalecarlicum* Lindström, p. 34, pl. 1, fig. 22; pl. 2, fig. 8.

Holotype. Lindström, 1880, pl. 2, fig. 8; RM Cn 57149, Styggforsen Limestone, Styggforsen, Siljan district, Dalecarlia, central Sweden; Telychian.

Material studied. The description is based on Lindström's (1880, pl. 1, fig. 22; pl. 2, fig. 8) illustrations of the type specimen and on the longitudinal thin section of the holotype (RM Cn57149); his transverse section is presumed lost. Dr B. Neuman (pers. comm.) has searched for more material in the type area without success.

Distribution. Central Sweden; Telychian.

Diagnosis. Fasciculate, possibly peripheral nonparricidal increase; corallites slender, less than 10 mm in diameter containing 22–23 major septa; prominent axial space; minor septa weakly developed; tabularium regularly arranged broad, flat-topped axial series and narrow, closely spaced, sagging periaxial series of tabellae; dissepiments elongate in one or two rows.

Description. The specimen from which the slide was cut is not available. The longitudinal section has the central corallite abutted on one side by the dissepimentarium of another and on the other side by the apparent margin of an offset (text-fig. 8B). This presumed offset shows the early stage of what is possibly a narrow row of flat tabellae beside the neo-wall, which is inserted on top of a dissepiment and which is not continuous with that of the parent. If these relations are correctly interpreted then the budding is peripheral nonparricidal. Immediately before the budding the corallite is 10 mm wide and at the top of the section it is 9.5 mm.

The transverse section is not available. Lindström (1880, pl. 1, fig. 22) shows 22 or 23 major septa that are smooth, straight and extend 0.8 the corallite radius to the axis where their axial tips may be turned aside, leaving an axial space. Minor septa are poorly developed as segments on the interseptal dissepiments between some major septa.

In longitudinal section the tabularium is very regularly developed and is well differentiated from the dissepimentarium. It shows axial series of broad flat tabellae with strongly downturned peripheral parts that are based on the tabellae below. There are 14–18 in 5 mm vertically. Between this zone and the dissepimentarium is a narrow periaxial series of slightly concave upward tabellae (17–19 per 5 mm) forming an exceptionally regular periaxial trough (Text-fig. 8B). Dissepiments are very irregular in size and shape, some twice as broad as others and varying from globose to elongate. The tabularia are 0.6–0.7 the corallite diameters and the axial series is 0.8 the diameter of the tabularium.

Remarks. *E.?* *dalecarlicum* cannot be adequately evaluated on the basis of the single longitudinal section of the holotype available for study. The possible occurrence of nonparricidal budding indicates a generic assignment other than *Entelophyllum*.

Genus PETROZIUM Smith, 1930

1930 *Petrozium* Smith, p. 307.

Type species. By original designation, *P. dewari* Smith, 1930, from the Pentamerus Beds of Shropshire, England; early Telychian.

Diagnosis. Phaceloid, corallites slender, cylindrical; increase presumably peripheral, nonparricidal. Septa long, grouped at axis or slightly withdrawn, thin or slightly thickened, commonly zigzag but rarely carinate in dissepimentarium. Tabularium strongly domed, tabulae complete with central area flattened or sagged and with outturned edges, or commonly incomplete with outermost tabellae forming a distinct series producing a periaxial trough. Dissepimentarium relatively narrow, dissepiments small, interseptal.

Remarks. Smith (1930) introduced *Petrozium* for one species described from a limited number of specimens and no further material has become available (see discussion of *P. dewari*). The genus has been variously interpreted by subsequent revisors. In his description of the type species, Smith (1930, p. 308) recognized the similarity, in longitudinal section, of *Petrozium* to *Entelophyllum* but did not elaborate on how they were to be distinguished and some authors have considered them synonymous.

Smith (1930) described the increase as marginal nonparricidal but we have not been able to confirm this in the material still available. If this is correct, then it contrasts with the typical parricidal mode of increase in *Entelophyllum* and resembles *Donacophyllum* Dybowski, 1876, but lacks the lonsdaleoid dissepiments characteristic of the latter genus.

Kaljo (1958) and Fedorowski and Gorianov (1973) both recognized the similarity between *P. dewari* and *Donacophyllum losseni* Dybowski, 1874, from the Llandover of Estonia. Kaljo referred the Estonian form to the genus *Petrozium*, and Fedorowski and Gorianov questionably included *P. dewari* in the synonymy of the Estonian species which they referred to *Entelophyllum*. The latter authors described six specimens of *P. losseni* from Eichwald's collection and noted that increase was peripheral nonparricidal. Apart from this, *P. losseni* resembles other species of *Entelophyllum* in which the major septa are thin, straight, and somewhat withdrawn from the axis leaving a conspicuous axial space such as that found in *E. fasciculatum*. In its early growth stages the septa may join at the axis as shown by Fedorowski and Gorianov (1973, fig. 6). The relatively narrow dissepimentarium and the incomplete development of the periaxial series of tabellae separate both *P. dewari* and *P. losseni* from *E. articulatum* but those features are found in varying degrees in other species of *Entelophyllum*.

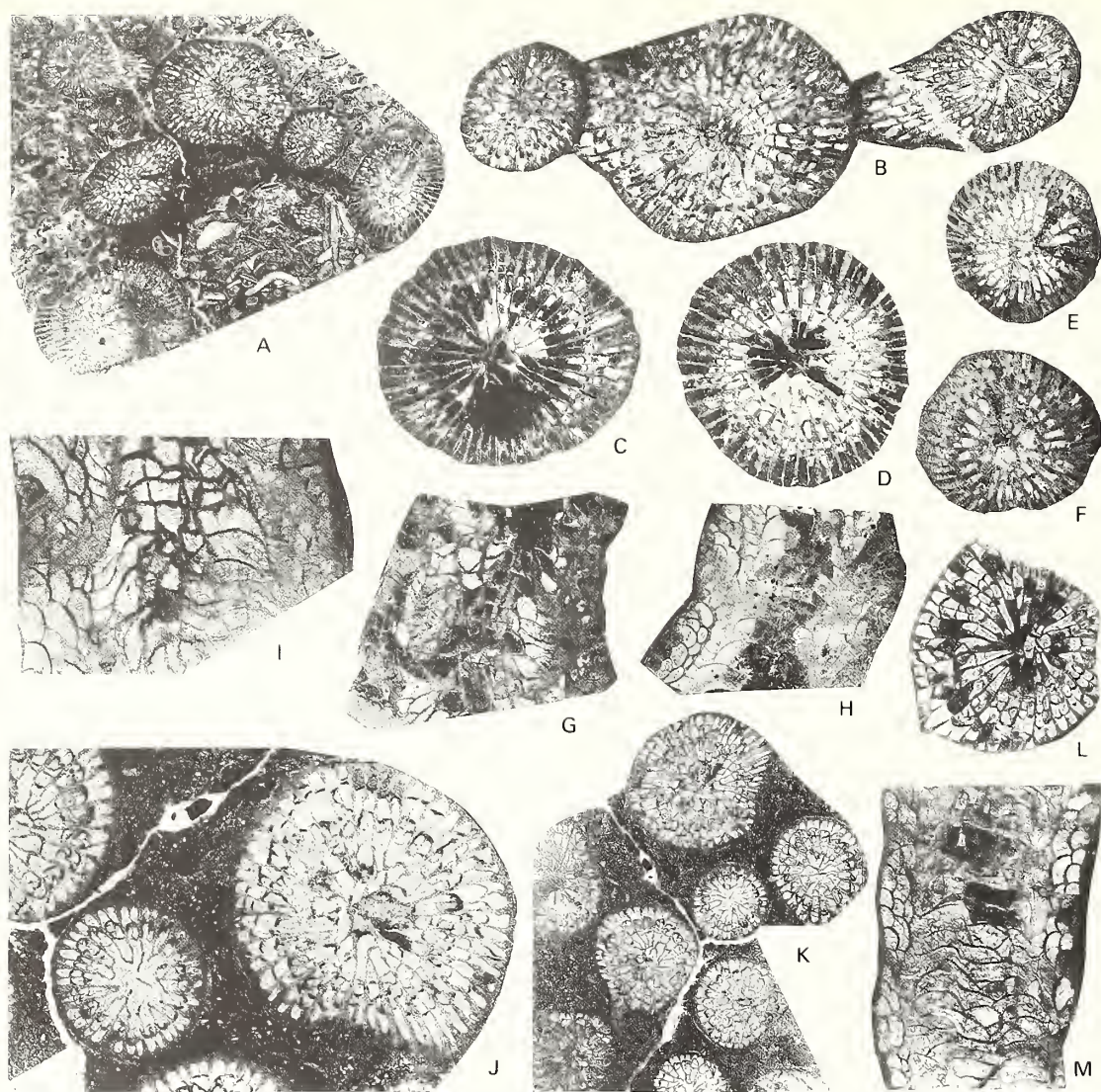
Smith (1930, p. 307) described the development of stereome between the axial ends of the longer major septa as forming with them an axial structure. Merriam (1972, 1973) considered the development of an incipient axial structure as a significant generic character of *Petrozium*. As seen in the Gotland species of *Entelophyllum* the withdrawal of the axial ends of the major septa from the axis is very variable within species as well as between species. Examination of the type material of *P. dewari* shows that the grouping of septa near the axis is common but the development of an incipient axial structure is rare.

Until the type species is better known *Petrozium* is maintained for those species similar to *Entelophyllum* but with nonparricidal increase, relatively narrow dissepimentarium, incomplete development of the periaxial series of tabellae, and lacking lonsdaleoid dissepiments.

Petrozium dewari Smith, 1930

Text-fig. 9A-M

v*1930 *Petrozium dewari* Smith, p. 307, pl. 26, figs 20-28.



TEXT-FIG. 9. *Petrozium dewari* Smith. A-F, Pentamerus Beds, right bank Morrells Wood Brook, 275 m NNE of Morrells Wood Farm, 1.6 km NNW of Buildwas, Shropshire; A and B, GSM PF4618 (holotype); transverse sections; $\times 2$, $\times 4$, respectively; C, GSM PF4622a, transverse section in upper part of corallite, $\times 4$; D, GSM PF4622b, transverse section, $\times 4$; E, GSM PF4622d, transverse section, $\times 4$; F, GSM PF4622e, transverse section showing septa slightly thickened in early growth stage, $\times 4$. G, GSM PF4619, longitudinal section, $\times 4$. H, GSM PF4623, longitudinal section, $\times 4$. I-M, Saugh Hill Group, Woodland Point, Girvan, Ayrshire; I-K, SM A15217; I, longitudinal section, $\times 4$; J and K, transverse sections, $\times 4$, $\times 2$ respectively; L and M, SM A15215; L, transverse section, $\times 4$; M, longitudinal section, $\times 4$.

Holotype. Smith, 1930, pl. 26, fig. 22; GSM 48674 (thin section PF4618), Pentamerus Beds, Morrells Wood Brook, 1.6 km NNW of Buildwas, Shropshire, England; early Telychian.

Material studied. The holotype and most of Smith's (1930) material is from the *Calostylis* limestone, a thin 10-15 cm thick bed of limestone in the Pentamerus Beds, at the type locality (seven specimens; figured: GSM

PF4618 (holotype); GSM PF4619, PF4622a-d, PF4623 (paratypes)); Smith's collection from the upper part of the Hughley Shale in the north bank of the Severn River, 366 m southeast of the church, Buildwas, Shropshire (one specimen); Saugh Hill Group, Woodland Point, Girvan, Ayrshire, Scotland (two specimens; figured: SM A15215, 15217).

Distribution. England: Telychian; Scotland: Llandovery (?Rhuddanian).

Diagnosis. Dendroid, almost placeloid; corallite diameter typically 8–10 mm; most of the 28–30 major septa meet at the axis or join in groups just short of the axis; minor septa 0.4–0.6 the length of major; septa slightly thickened or lightly carinate in outer dissepimentarium; tabularium biserial, axial tabellae arched, periaxial series incompletely developed; dissepiments globose, irregular in size, in two or three vertical rows.

Description. The holotype is a thin upper part of a dendroid to phaceloid corallum showing eight corallites imbedded in a coarse bioclastic limestone so that no calices are exposed. The corallites are 8–10 mm in diameter and appear to be cylindrical. Adjacent corallites are separated by as much as 5 mm but in section they are touching in places suggesting they have lateral expansions that spread out to support the corallite against adjacent ones. The mode of increase is not evident.

The other specimens are all fragments of isolated cylindrical corallites. Some show slight lateral expansions of the corallite as though they were part of a phaceloid coralla.

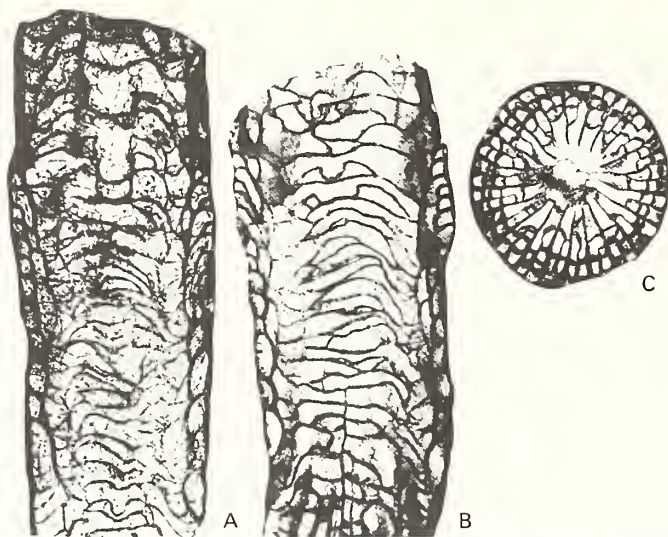
Septa are commonly thin, straight, radially arranged in two orders with 28–30 in each. Major septa extend well into the tabularium and may meet at the axis or join in groups of three or four just short of the axis (Text-fig. 9C, D). In the holotype, an axial plane is evident across which opposing septa join so that the corallite has a bilateral symmetry. Only in the largest corallite of the holotype, the axial ends of the septa are slightly thickened and in places confluent, forming a small open axial structure (Text-fig. 9B). Minor septa are 0.4–0.6 the length of the major with a few contraclined. In the dissepimentarium, both orders of septa are: commonly straight and thin; rarely straight, slightly thickened and noncarinate; or rarely thin, slightly zigzag with short carinae.

The tabularium and dissepimentarium are clearly differentiated with the former consisting of an axial and periaxial series of tabellae. Axial tabellae are domed with the central part flattened or depressed in some and their peripheral edges sharply downturned. A series of horizontal or slightly sagging tabellae, closely spaced with 20–26 per 5 mm vertically, span the space between the downturned peripheral edges of the axial tabellae and the dissepimentarium, forming a periaxial trough (Text-fig. 9H). The dissepimentarium is composed of irregular sized, globose dissepiments, horizontally based at the periphery and steeply declined axially, and arranged in two or three irregular rows with 8–10 in each row per 5 mm vertically.

Septa are composed of fine monacanthi arranged in one series. Trabeculae are directed upwards at a small angle to the vertical at the periphery and flatten axially so that at the tabularium/dissepimentarium boundary they are within 20° of the horizontal and then towards the axis they steepen considerably. Thickenings of the septa and the short carinae are only the lengthening of fibres of the trabeculae.

Remarks. Description is based on the same material as described by Smith (1930), excluding specimen GSM 48721. We have twice visited the type locality without finding any additional material referable to this species. Also, we have not recognized this species in our collections from other upper Llandovery localities of Shropshire.

Smith (1930) included in this species specimen GSM 48721 (PF4529–30) from the type locality. It is a fragment of a much larger corallite (20 mm in diameter) and whether or not it is a corallite from a colony or a worn solitary form is not apparent. It seems unlikely that it is conspecific with the smaller cylindrical corallites. A fragment of a phaceloid corallum (Text-fig. 9I–K) and an isolated cylindrical corallite (Text-fig. 9L and M) from the Saugh Hill Group, Woodland Point, Girvan, Ayrshire (SM A5215, A5217) are very similar to the Shropshire material. The Scottish material may be Rhuddanian in age and thus somewhat older than the type material. We have searched the Woodland Point sequence for additional material but without success. Several larger specimens are known from the same collection but whether solitary or from fasciculate coralla is not known and they are not included in the species at this time.



TEXT-FIG. 10. *Petrozium losseni* (Dybowski), EGM Co1282, Tamsalu Formation, Juuru Horizon, Suuremyiza (near Grossenkhof), Isle of Hiiumaa, Estonia. A and B, longitudinal sections, $\times 4$. C, transverse section, $\times 4$.

Petrozium losseni (Dybowski, 1874)

Text-fig. 10A-C

- 1874 *Donacophyllum lossenii* Dybowski, p. 464, pl. 4, fig. 6, 6a, b.
 1958 *Petrozium losseni* (Dybowski); Kaljo, p. 114, pl. 4, figs 11-17.
 1973 *Entelophyllum losseni* (Dybowski); Fedorowski and Gorianov, 1973, p. 20, pl. 4, fig. 5a-c; text-figs 6 and 7.

Holotype. Dybowski, 1874, pl. 4, fig. 6, 6a, b; EGM Co1282; Tamsalu Formation, Juuru Horizon, at Suuremyiza (near Grossenkhof), Isle of Hiiumaa, Estonia; Rhuddanian.

Material studied. This species is interpreted from published data and from photographs of the holotype kindly supplied by Dr D. Kaljo (figured: EGM Co1281, holotype). It is known from several localities on Hiiumaa Island. Kaljo (1970) listed it as only occurring in the Juuru Horizon (Rhuddanian) in Estonia. Two specimens in the Eichwald Collection are labelled as from Lode on Saaremaa Island and thus from the Kuressaare Horizon (Ludfordian) but Fedorowski and Gorianov (1973, p. 23) suggest this is an error. The same authors list another of Eichwald's specimens from Viljandi in southern Estonia and suggest it is probably from an erratic boulder.

Distribution. Estonia: Rhuddanian.

Diagnosis. Phaceloid, peripheral nonparricidal increase; corallite diameters 6-7 mm, maximum 9.5 mm; major septa number 23-26, straight, smooth, withdrawn from the axis leaving axial space or extending to or almost to axis, several adjacent septa may be grouped just short of axis; minor septa half length of major, not contratigent. Tabularium broad, biserial with narrow periaxial trough; dissepiments small, globose in one to three rows.

Remarks. *P. losseni* is very similar to *P. dewari*, and Fedorowski and Gorianov (1973) suggested that the two might be synonymous. *P. losseni* is here distinguished from *P. dewari* by the thinner septa, especially in the tabularium, absence of any septal carination, thicker corallite walls, and typically a narrower dissepimentarium. Tabularia of both species are very similar but there appears to be more complete tabellae and less complete development of the periaxial series of tabellae in *P. losseni*. The Estonian *P. losseni* is from slightly older strata (Rhuddanian) than the type material of

P. dewari of England (early Telychian). *P. losseni* may be of similar age to the Scottish form referred to *P. dewari* and resembles it in that the major septa may be withdrawn from the axis and are similarly grouped. However, the septa of the Scottish material are thicker and more like the type material of *P. dewari*.

P. losseni differs from the Llandovery *E. dendroides* from Gotland by its phaceloid habit, withdrawal of septa from the axis, more complete and less densely spaced tabulae, and narrower dissepimentarium.

Genus PROHEXAGONARIA Merriam, 1973

1973 *Entelophylloides* (*Prohexagonaria*) Merriam, p. 50.

Type species. By original designation, *Entelophylloides* (*Prohexagonaria*) *occidentalis* Merriam, 1973, from bottom of unit 3, Roberts Mountains Formation, northwest side Roberts Creek Mountain, Nevada, U.S.A.; ?Pridoli Series.

Diagnosis. Cerioid or subcerioid; increase peripheral nonparricidal; septa thin with inconspicuous asymmetrical carinae, long, some reaching the axis; tabulae closely spaced, complete or typically incomplete, axially arched and outturned at their periphery; dissepiments globose, small, increasing in axial inclination away from the periphery, typically interseptal, rarely lonsdaleoid.

Remarks. Merriam (1973) originally defined *Prohexagonaria* as a subgenus of *Entelophylloides* Rukhin, 1938 (type species *Columnaria inequalis* Hall, 1852), but that genus is a ptenophyllid coral and possibly synonymous with *Xystriphyllum* Hill, 1939. *Prohexagonaria* is generally similar to *Entelophyllum* in internal character but is cerioid and has nonparricidal increase. In the latter feature it shows resemblance to the phaceloid *Donacophyllum* but in *Prohexagonaria* lonsdaleoid dissepiments are rare except in the extended corners of some corallites. Until the modes of increase in all of the cerioid forms with typical entelophylloid internal structure are better known, *Prohexagonaria* is included in the Entelophyllidae.

Prohexagonaria may be congeneric with *Tenuiphyllum* Soshkina, 1937 (type species *T. ornatum* Soshkina, 1937, from the Elkinskii Horizon, right bank of River Vya, near Elkino, eastern slopes of the Urals, USSR; see Ivanovskii and Shurygina 1975, p. 23). Pedder (1976, p. 290) indicates that the two genera may not be synonymous as *T. ornatum* shows significantly expanded septal bases.

Prohexagonaria favia sp. nov.

Plate 10, figs 1–4

v1929 ?*Xylodes* sp. Smith and Tremberth, p. 366, pl. 8, fig. 1.

v1973 *Entelophylloides* (*Prohexagonaria*) sp., Merriam, pl. 9, fig. 5.

Holotype. Original of Smith and Tremberth, 1929, pl. 8, fig. 1; RM Cn57005, two parts of specimen plus three thin sections; two parts of the holotype plus two thin sections are in the BMNH collection (R26168–26171); from upper Visby Beds, Norderstrand, Visby, Gotland; early Sheinwoodian.

Material. The holotype is the only known specimen.

Distribution. Gotland: early Sheinwoodian.

Diagnosis. Cerioid, increase peripheral nonparricidal; corallites 10–15 mm in diameter; major septa number 21–25, long, extending to or almost to axis, only rarely confluent, commonly interrupted at periphery; minor septa weakly developed, discontinuous in places; tabularium weakly biserial with incomplete periaxial trough; dissepiments irregular in shape and size.

Description. The holotype is a fragment of a cerioid corallum and measures 15 × 10 cm in cross section and 5 cm high. Corallites are five- to six-sided and measure 10–15 mm in diameter. Offsets common along

boundaries between corallites especially on corners between three adjacent corallites (Pl. 10, fig. 2) so that it is difficult to determine from which corallite they have arisen. In longitudinal view they appear to arise from the extreme outer edge of the dissepimentarium. Increase is nonparricidal.

Septa are long, thin, radially arranged in two orders. Major septa number 22–25 and extend right to or almost to the axis (Pl. 10, fig. 2). In a few cases one and even two major septa project into axial area further than the others. Major septa thin slightly towards periphery and in extended corners before budding they may be incomplete resting on larger dissepiments. Minor septa may be thin and complete, 0.3–0.4 the length of the major septa, but more commonly they are incomplete and represented as short segments based on herringbone dissepiments and more strongly developed in inner dissepimentarium than in outer parts. The septa are noncarinate. In small offsets some of the septa are discontinuous in the dissepimentarium.

Tabularium is 0.6–0.7 diameter of corallite in width and is well marked from the dissepimentarium. It consists of small globose tabellae arranged in a domed or flattened domed axial series 0.7 diameter of tabularium, and flatter and smaller tabellae forming a periaxial series abutting dissepimentarium (Pl. 10, fig. 4). Periaxial series does not form a continuous periaxial trough. There are up to 12 tabellae in both series in 5 mm vertically. Dissepimentarium is composed of irregular sized dissepiments varying from small globose, less than 0.5 mm across, to elongated moderately inclined up to 3 mm in length spanning the complete dissepimentarium.

Septa are composed of one series of fine trabeculae (5–6 in 1 mm in median longitudinal section) that are inclined upwards and inwards in the dissepimentarium and steepening to near vertical in the tabularium.

Remarks. This species is not similar to any known European entelophylloid ceroid coral. It is similar to the type species of the genus, which is from considerably younger strata in western North America, differing only in that *P. favia* has noncarinate septa and its tabularium is considerably wider.

Prohexagonaria gotlandica sp. nov.

Plate 10, figs 5–8

Holotype. RM Cn66198, Hamra Beds, Storborg 1, Hoburgen, southern tip of Gotland; late Ludfordian.

Material. Only the holotype is known.

Distribution. Gotland: late Ludfordian.

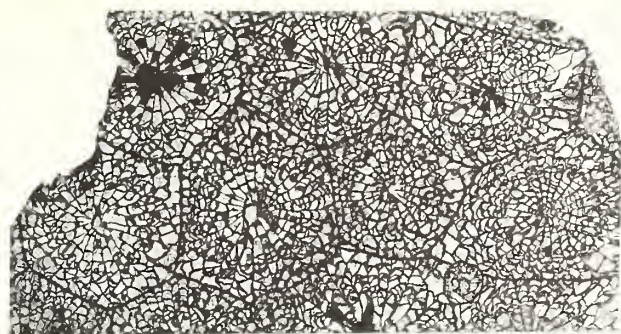
Diagnosis. Cerioid, increase peripheral nonparricidal; corallites 8–12 mm diameter; major septa number 20–25, extending almost to axis, thickened in the inner dissepimentarium, zigzag and carinate in outer dissepimentarium; minor septa well developed, carinate; tabularium biserial with distinct periaxial trough; dissepiments globose, irregularly arranged with outer series horizontally based and inner ones steeply inclined axially.

Description. Holotype is a fragment (8–10 cm in section and up to 5 cm in height) of a larger corallum. Corallites are five- to six-sided and measure 8–12 mm in diameter. Offsets arise in the expanded corners of the corallites (Pl. 10, fig. 6) and quickly expand so that the corallum resumes a regular cerioid form. Twenty calices are preserved and from these and the sections, all increase appears to be peripheral nonparricidal.

EXPLANATION OF PLATE 10

Figs 1–4. *Prohexagonaria favia* sp. nov. RM Cn57005 (holotype), upper Visby Beds, Nordenstrand, Visby, Gotland. 1 and 2, transverse sections, $\times 2$, $\times 4$, respectively. 3 and 4, longitudinal sections, $\times 2$, $\times 4$, respectively.

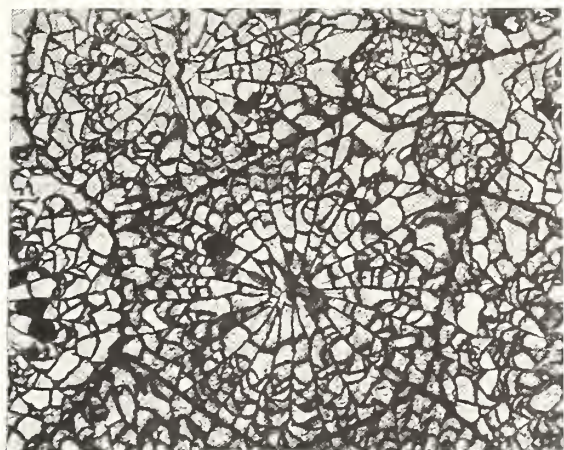
Figs 5–8. *Prohexagonaria gotlandica* sp. nov. RM Cn66198 (holotype), Hamra Beds, Storborg 1, Hoburgen, southern tip of Gotland. 5 and 6, transverse sections, $\times 2$, $\times 4$, respectively. 7 and 8, longitudinal sections, $\times 2$, $\times 4$, respectively.



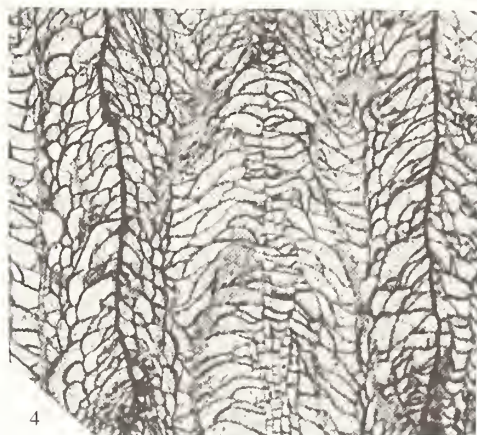
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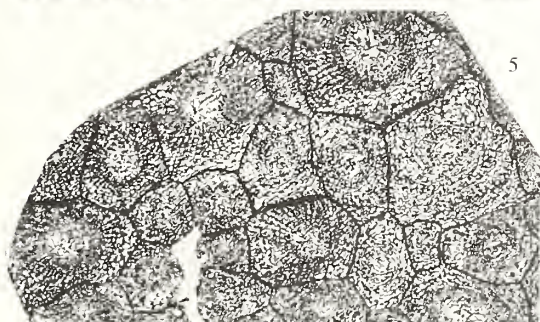
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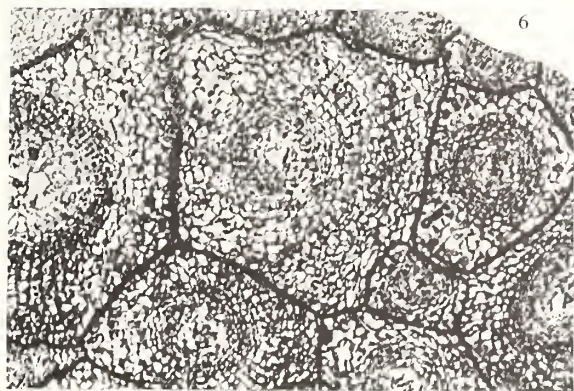
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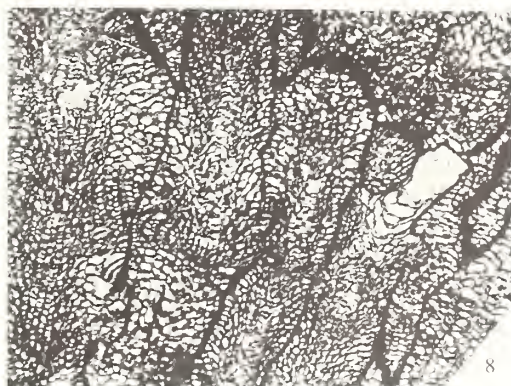
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Major septa number 20–25 with one corallite having 30. They are slightly thickened in the inner dissepimentarium and thin in the tabularium where they are straight to flexuose and extend almost to the axis, leaving a narrow axial space (Pl. 10, fig. 6). Minor septa are slightly thinner than the major, 0.7–0.8 the length of major, and project into tabularium a short distance. All septa are zigzag in outer dissepimentarium and may carry short carinae. Carination varies from absent to light in outer dissepimentarium, light to heavy in middle dissepimentarium, and light on thickened parts in the inner dissepimentarium. Only in extended corners where offsets are forming do septa become discontinuous.

The longitudinal section is oblique but locally shows a typical entelophylloid tabularium half the radius of the corallite (Pl. 10, fig. 8). Axial series consists of flattened tabellae strongly downturned at their margins; the downturned edges may flatten out to meet inner dissepimentarium horizontally or they are surrounded by a series of flat to sagging tabellae. A periaxial trough is well-developed. Dissepiments are globose, varying from 0.5–1.0 mm across, not arranged in regular vertical rows.

Remarks. This species differs from *P. favia* in having distinctly smaller corallites, better developed septa that are commonly carinate, and a narrower tabularium with a well developed periaxial trough.

Family KYPHOPHYLLIDAE Wedekind, 1927

Genus DONACOPHYLLUM Dybowski, 1874

1874 *Donacophyllum* Dybowski, p. 460.

1927 *Kyphophyllum* Wedekind, p. 19.

Type species. Chosen by subsequent designation of Wedekind, 1927, p. 34, *Donacophyllum schrenkii* Dybowski, 1874, from Raikküla Horizon of Estonia; Aeronian, middle Llandovery.

Diagnosis. Phaceloid, typically with nonparricidal peripheral increase; periodic rejuvenescence of corallites, reflecting expansions and subsequent contractions of dissepimentarium; major septa long and thin, a little withdrawn from axis, one may be longer; tabularium wide, domed, commonly with depressed axial area and marginal periaxial trough; dissepiments commonly lonsdaleoid.

Remarks. We follow Hill (1981) in placing *Kyphophyllum* in the synonymy of *Donacophyllum*. We have not made a comprehensive study of these genera. Gotland species here included in *Donacophyllum* are close to *Entelophyllum* in septal and tabularial characters but increase is lateral nonparricidal and lonsdaleoid dissepiments are much better developed.

Donacophyllum neumani sp. nov.

Plate 11, figs 1–8

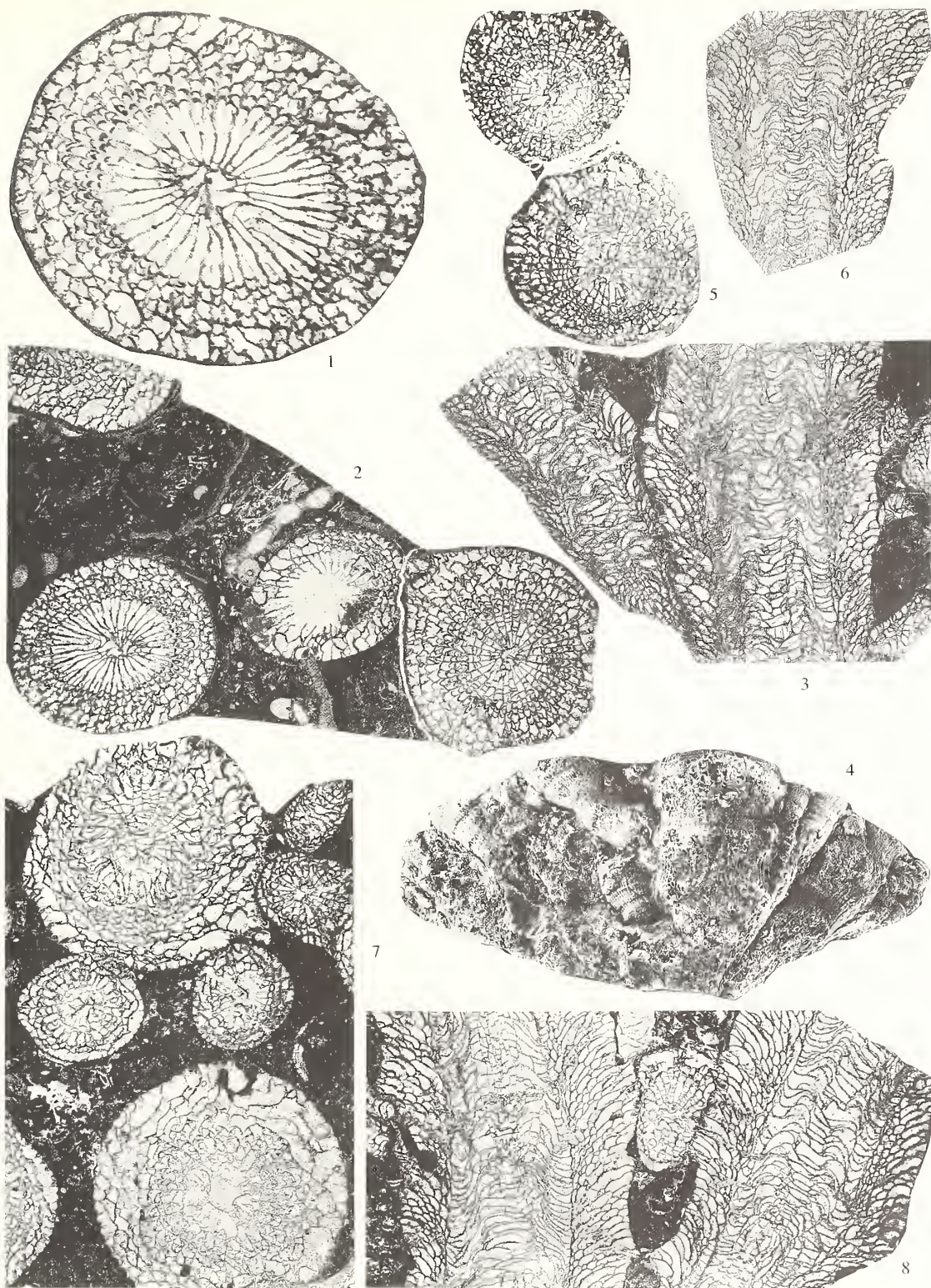
Holotype. RM Cn66199, from a limestone of the Slite Beds, towards top of cliff section of Lerberget 1, Stora Karlsö, Gotland; late Sheinwoodian or early Homerian.

Material studied. This species is known only from the type locality (five specimens; figured: RM Cn66199 (holotype), Cn66200, Cn66201).

Distribution. Gotland: late Sheinwoodian or early Homerian.

EXPLANATION OF PLATE 11

Figs 1–8. *Donacophyllum neumani* sp. nov., Slite Beds, Lerberget 1, south of lighthouse, western shore of Stora Karlsö, Gotland. 1–4, RM Cn66199 (holotype); 1 and 2, transverse sections, $\times 4$, $\times 2$ respectively; 3, longitudinal section, $\times 2$; 4, lateral view of corallum, $\times 1$. 5 and 6, RM Cn66200; 5, transverse section, $\times 2$; 6, longitudinal section $\times 2$. 7 and 8, RM Cn66201; 7, transverse section, $\times 2$; 8, longitudinal section, $\times 2$.



JELL and SUTHERLAND, *Donacophyllum*

Diagnosis. Fasciculate, flat, laterally flaring coralla; increase lateral nonparricidal; corallites up to 20 mm in diameter. Major septa 25–31, long, generally straight, smooth in tabularium, extending to within 1 mm of axis; slightly thickened in outer tabularium and inner dissepimentarium; may be carinate in dissepimentarium, interrupted by lonsdaleoid dissepiments in outer dissepimentarium; minor septa absent to weakly developed. Tabularium half diameter of corallite, biserial with well developed periaxial trough, axial part of domed tabularial floor sagged. Dissepiments medium to large sized, highly irregular, not in regular vertical rows with larger lonsdaleoid dissepiments at periphery.

Description. Holotype is a flat laterally flaring corallum 100 mm in diameter and 70 mm high. Corallites are ceratoid up to 20 mm in diameter and 20–50 mm in height. Increase is lateral, nonparricidal with offsets arising from extreme peripheral rim of the calice (Pl. 11, fig. 3). Offsets turn outwards soon after initiation and diverge up to 30° from parent (Pl. 11, fig. 4). No lateral expansions between corallites have been observed. Other specimens from type locality show same corallum form and corallite shape and size.

Major septa number 25–31, are moderately straight and smooth in tabularium, and extend to within 1 mm of the axis. In a few corallites, a single septum extends into axial space and in some, two or three adjacent septa are confluent giving small groupings of septal ends about the axial space. Some show a slight thickening in outer tabularium and/or inner dissepimentarium. Septa are commonly discontinuous in outer dissepimentarium where they are interrupted by irregular lonsdaleoid dissepiments. They may become zigzag and carry short carinae, especially along their peripheral parts. Minor septa mostly poorly developed, much thinner and more irregular than adjacent major septa and commonly lacking from parts of some corallites. They project only slightly into tabularium. In young, small corallites septa of both orders are smooth, straight and interrupted peripherally by large dissepiments.

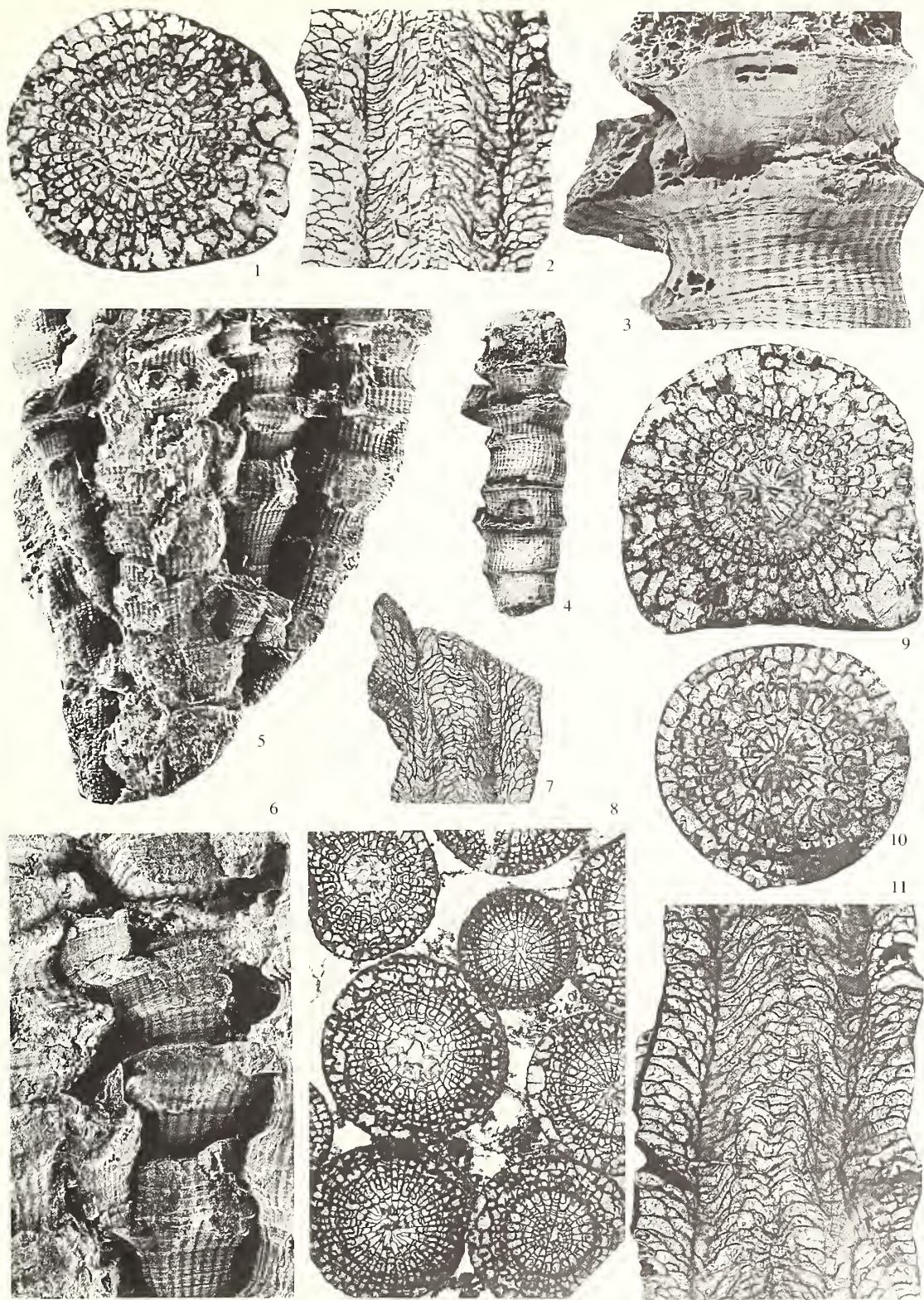
Wide tabularium, 0.4–0.5 corallite diameter in width, is distinctly separate from dissepimentarium. It is biserial with axial tabulae centrally domed but with an axial depression, downturned steeply at margin of this central area and then flattening out or even concave peripherally to give a prominent periaxial trough. Central tabellae are flat or slightly concave upwards and number 8–10 in 5 mm vertically. They are surrounded by more globose tabellae that have steeply downturned outer edges that rest on the ones immediately below. Periaxial tabellae may span interval between domal part of tabularium and dissepimentarium. These are flat or concave upwards and number 10–12 for 5 mm vertically. Dissepiments are mostly elongated, adaxially inclined, variable in size, and not arranged in regular vertical series. Lonsdaleoid dissepiments common in peripheral parts.

Septa consist of one series of monacanthine trabeculae that are directed upwards and inwards across the dissepimentarium at approximately 45°. They tend to flatten to nearly horizontal in periaxial region of tabularium but steepen to within 30° of vertical in axial region. Fibers within trabeculae diverge at only a slight angle from axis so that fibers appear to parallel trabeculae, and boundaries and axes of individual trabeculae cannot be distinguished. Carinae are lateral extensions of the fibers of the trabeculae and, where present, are 0.2–0.5 mm apart, centre to centre.

Remarks. *D. neumani* is distinguished from *E. articulatum*, also from the Slite Beds, primarily by its lateral nonparricidal increase and flaring growth form of the corallum, and major development of lonsdaleoid dissepiments. It differs from *D. wallstenense* in the flaring growth form of the corallum and much larger size of the corallites.

EXPLANATION OF PLATE 12

Figs 1–11. *Donacophyllum wallstenense* sp. nov. 1–4, RM Cn10637, Slite Beds, Stora Karlsö, Gotland; 1, transverse section, $\times 4$; 2, longitudinal section, $\times 4$; 3 and 4, lateral view of corallite; 3, showing offset arising from expansion of corallite, $\times 4$; 4, showing series of expansions, $\times 1$. 5–8, RM Cn11963 (holotype), Slite Beds, Stumra stenbrott, Wallstena Parish, Gotland; 5 and 6, lateral view of corallum showing lateral nonparricidal increase, $\times 1$, $\times 2$, respectively; 7, longitudinal section, $\times 2$; 8, transverse section, $\times 2$. 9–11, Slite Beds, Stora Karlsö, Gotland; 9, RM Cn10643, showing lateral expansion, $\times 4$; 10 and 11, RM Cn10635; 10, transverse section, $\times 4$; 11, longitudinal section, $\times 4$.



JELL and SUTHERLAND, *Donacophyllum*

Donacophyllum wallstenense sp. nov.

Plate 12, figs 1–11

Holotype. RM Cn11963, Slite Beds, Stumra stenbrott (stone quarry), Wallstena Parish, Gotland; Slite Group; late Sheinwoodian to early Homerian.

Material studied. Holotype (RM Cn11963) is the only specimen from Wallstena. Additional specimens referred to this species are also apparently from the Slite Group, from an unknown locality on the island of Stora Karlsö, Gotland (14 Specimens, RM Cn10635–10647; figured: RM Cn10635, Cn10637, Cn10643). Some of the specimens from Stora Karlsö show small remnants of gray marl and thus they may have come from the lithology of that type observed in the lower part of the Slite Group below the more greenish limestone from which were collected the type specimens of *D. neumani* sp. nov. An additional occurrence is questionable: 2 km southeast of ferry at Broa, Isle of Fårö, Gotland.

Distribution. Gotland: late Sheinwoodian to early Homerian.

Diagnosis. Phaceloid, tall coralla; increase lateral nonparricidal; corallites up to 15 mm in diameter. Major septa number 23–27, typically smooth leaving a small open axial area into which a single septum may extend; may be distinctly thickened in outer tabularium and/or in dissepimentarium; may be interrupted by lonsdaleoid dissepiments in outer dissepimentarium. Tabularium half diameter of corallite, biserial with a well developed periaxial trough. Dissepiments variable in size and distribution.

Description of holotype. Holotype is a fragment of a tall, phaceloid corallum up to 90 mm in height and 75 mm across, consisting of close to 20 corallites. Corallites are long, subcylindrical and closely packed. They show semi-regular expansions and contractions at a spacing of 10–15 mm apart (Pl. 12, fig. 5). Method of increase is lateral and nonparricidal, with the offset diverging at outer lip of expansion but becoming immediately parallel to parent (Pl. 12, fig. 6).

Major septa number 23–27 and they extend to within 1 mm of axis. Commonly one long septum bisects the narrow axial space (Pl. 12, fig. 8). Septa mostly smooth and straight throughout their length but a few are zigzag in dissepimentarium and a few are carinate. In some corallites they are rather markedly thickened in the outer tabularium and less commonly in dissepimentarium. Septa thickening is lacking in some corallites. Peripherally septa may be discontinuous or interrupted locally by lonsdaleoid dissepiments, especially at lateral expansions. Minor septa extend slightly into tabularium and tend to have a similar pattern in dissepimentarium to major septa or they may be more discontinuous.

Tabularium is half diameter of corallite and is distinctly delineated from dissepimentarium. Central highly domed area may or may not have a central depression. Tabulae steeply downturned periaxially to form a distinct periaxial trough (Pl. 12, fig. 7). Axial tabellae number about 8 in 5 mm vertically. Axial part of domal area consists of flat or slightly depressed tabellae bordered by more globose plates whose peripheral edges are steeply downturned. Flat to deeply sagging tabellae span space between central domal area and dissepimentarium. Dissepiments are variable in size and shape and range from globose to more elongate, peripherally lonsdaleoid dissepiments are common. Width of dissepimentarium varies markedly because of expansions and contractions of corallite.

Microstructure is similar to that described in *D. neumani*.

Description of other material. Specimens from the island of Stora Karlsö that are referred to this species consist of 14 broken individual corallites (Pl. 12, figs 1–4, 9–11). They are similar to the smaller corallites of holotype in number of septa, nature of biserial tabularium and variable dissepimentarium. They differ from holotype primarily in lack of pronounced thickening in outer tabularium in some corallites, in greater tendency of septa to extend to axis, and in more common occurrence in dissepimentarium of zigzag septa and carinae.

Remarks. *D. wallstenense* differs from *D. neumani* in the upright growth form of the corallum, the distinctly smaller size of the corallites, and the greater development of thickening at the outer tabularium and dissepimentarium.

Acknowledgements. We wish to thank the many persons who have aided us in obtaining a better understanding of the entelophylloid corals. In particular, we thank Björn Neuman (University of Bergen) and the late Anders Martinsson (University of Uppsala) for having shown us the Silurian stratigraphy of Gotland and for having taken us to many collecting localities; Björn Neuman for the loan of some of his coral collections from Gotland; Dr V. A. Sytova for having shown us in Leningrad her extensive coral collections and for extensive information on the distribution of entelophylloid corals in the Soviet Union; Dr Dorothy Hill (University of Queensland) for her knowledgeable discussions on the relationships of Silurian coral genera; Dr D. L. Kaljo (Institute of Geology, Estonia) for information on Estonian coral distributions; Dr A. Galle (Ústřední ústav geologický) for photographs and information on the Czechoslovakian forms; and Dr Michael Bassett (National Museum of Wales) for information on the international correlations of Silurian stages. For the loan of specimens for study we are indebted to the curators of the museums listed at the beginning of the section on Systematic Palaeontology. We owe a particular debt of thanks to William W. Clopine (University of Oklahoma) who assisted us during the final preparation of the manuscript by both the preparation of critical thin sections and by photographing many of the specimens.

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Typescript received 9 May 1989

Revised typescript received 1 February 1990

BRACHIOPODS AND THE STRATIGRAPHY OF THE UPPER CAMPANIAN AND LOWER MAASTRICHTIAN CHALK OF NORFOLK, ENGLAND

by M. B. JOHANSEN and F. SURLYK

ABSTRACT. Thirty-four species of brachiopods are described from the Upper Campanian and Lower Maastrichtian Chalk of Norfolk. The Campanian–Maastrichtian boundary sequence in Norfolk is very poorly exposed and is condensed. However, the existence of a highly diverse micromorphic brachiopod fauna allows correlation with more complete and well-exposed sections elsewhere in northwest Europe, especially northwest Germany and Denmark. Most of the brachiopod zones established in continental northwest Europe can be recognized in Norfolk. These are from below: the *tenuicostata-longicollis* Zone (corresponding to the bulk of the Upper Campanian of Norfolk), the *longicollis-jasmundi* Zone (uppermost Campanian), the *acutirostris-spinosa* Zone (basal Maastrichtian), the *spinosa-pulchellus* Zone (middle part of the Lower Maastrichtian) and the *pulchellus-pulchellus* Zone (upper Lower Maastrichtian). The stratigraphical scheme of previous workers was essentially based on faunal and subordinate lithological criteria. This is revised within a strictly lithostratigraphical framework to avoid ambiguities. Eight members are recognized comprising, from below: Eaton Chalk, Weybourne Chalk (including Catton Sponge Bed at its top), Beeston Chalk, Paramoudra Chalk, Sidestrand Chalk, Trimmingham Sponge Beds, Little Marl Point Chalk, and Beacon Hill Grey Chalk Members.

HIGH diversity faunas of micromorphic brachiopods are well known from the Upper Cretaceous chalks of Denmark, Sweden, Germany and Poland (Steinich 1965, 1967, 1968*a, b*; Surlyk 1970*a, b*, 1972, 1973, 1974, 1975, 1982, 1984; Surlyk and Birkelund 1977; Surlyk and Johansen 1984; Bitner and Pisera 1979; Ernst 1984; Johansen 1986, 1987*a, b*, 1988), and a detailed brachiopod biozonation has been established for the Maastrichtian Stage. Washing of a large number of bulk samples collected in the Upper Campanian–Maastrichtian Chalk of Norfolk has yielded about 2200 specimens of brachiopods representing approximately thirty-five species. The occurrence of this fauna in the English Chalk makes it possible to correlate parts of the often poorly exposed Maastrichtian outcrops in Norfolk with the more completely exposed sections of continental northwest Europe, and to support previous correlations based on other faunal groups. Palaeoecological conclusions obtained by the study of the micromorphic fauna (Surlyk 1972) can also be extended to these parts of the English Chalk.

METHODS

Thirty-seven bulk samples were washed after boiling in a supersaturated Glauber-Salt solution following the method described by Surlyk (1972). Sample dry weight varied between 1 and 5 kg. The washed residues were sieved into 0.25–0.5 mm, 0.5–1.0 mm, and > 1.0 mm fractions, and the brachiopods were picked from the two latter fractions under a binocular microscope. The 0.25–0.5 mm fraction was in some instances checked for the earliest juvenile stages.

All specimens including the smallest juveniles were determined to species, and the minimum number of individuals was computed for each sample by adding to the number of complete shells the highest number of either dorsal or ventral valves. Ultrasonic cleaning was necessary when the details of shell ornamentation were hidden by adherent chalk. This was particularly the case with

material from the more indurated lithologies. SEM photographs were used for illustrative purposes, as normal photography is inadequate for illustrating finer details of rib sculpture and the pedicle foramen of the very small species. Preparation was done under a binocular microscope with a fine needle and brush, after attaching the specimen to a glass plate with 'Lakeside' cement.

The catalogued material is housed at the Geological Museum, University of Copenhagen. Material not catalogued belongs to a private collection of the second author of this paper (F.S.).

STRATIGRAPHY

The Campanian–Maastrichtian part of the Chalk in Norfolk is not very well known because of its incomplete exposure (Text-fig. 1). For much of the succession the sections are limited to widely scattered, often abandoned, chalk pits, and larger, glacially transported masses in coastal cliffs. This chalk was subdivided into a number of units by Brydone (1906, 1908, 1909, 1930, 1938). These units form the basis for the detailed geological map of Peake and Hancock (1970, pl. 2).

The nature of Brydone's stratigraphic units is somewhat unclear. Most of the subdivisions are named after a locality, although the fossil content is normally the main defining element. According to Wood (1988) the scheme is essentially palaeontological and the units of Brydone, as revised and updated by Peake and Hancock (1961, 1970), can be mapped out as faunal belts. The units are, however, in most cases characterized by a distinct lithology, or topped by a thin horizon of different lithology such as a hardground. They are redefined as lithostratigraphic units in the present paper, but it should be noted that the units recognized here are essentially equivalent to those of earlier authors even if they are conceptually different. Our aim in this revision is thus to introduce some consistency to the stratigraphical terminology.

The rank of the units is difficult to establish since the Upper Cretaceous Chalk of the North Sea and surrounding land areas has received little study from a lithostratigraphic point of view. Several formations have been recognized for the subsurface chalks of the North Sea (e.g. Deegan and Scull 1977; Svendsen 1979). These units are, however, of a very broad nature, and they are defined on the basis of petrophysical logs and relatively sparse core material from boreholes. They are difficult to correlate with exposed onshore chalk sequences.

The lithological differences between the individual units of the Chalk of Norfolk are relatively small and the thickness of the individual units usually amounts to a few metres only. The units can thus conveniently be treated as having member rank. The Chalk of Norfolk is generally of a more shallow-water nature than the North Sea Chalk, as witnessed by the common occurrence of single or compound hardgrounds and richer benthic faunas.

Lithostratigraphy

All localities described in the present paper expose Chalk of Late Campanian and Maastrichtian age; older sediments, including the 'Basal *mucronata* chalk' of Norfolk (Peake and Hancock 1970), are thus not dealt with in the following account. Since the lithostratigraphic units are given member rank (Text-figs 1 and 3) they should logically be grouped in one or more formations. This we leave, however, to students of the regional geology of eastern England. The description of the individual members is mainly based on Peake and Hancock (1970), Wood (1967, 1988), and our own observations.

Eaton Chalk Member

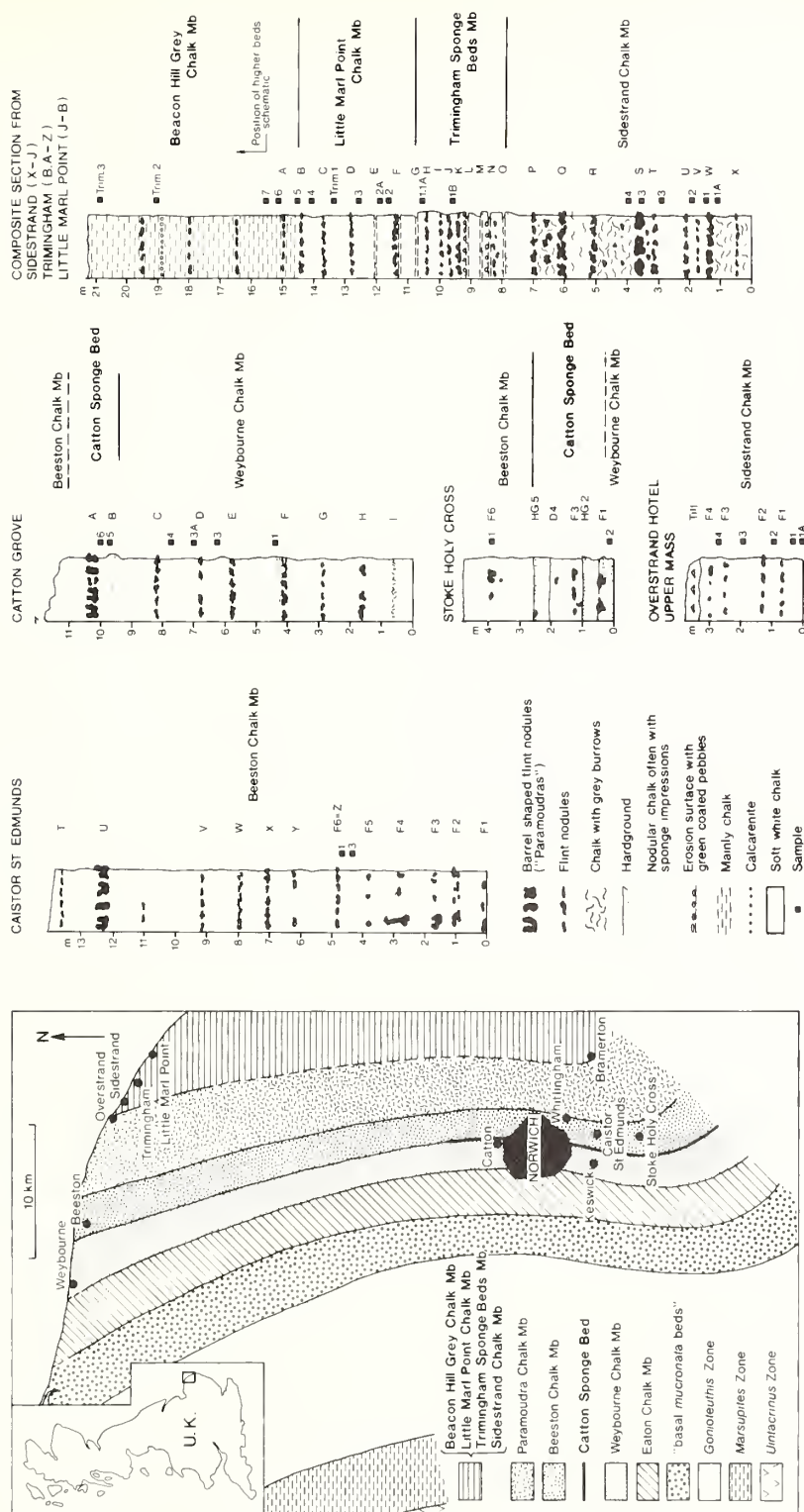
Name. After underground workings at the village of Eaton (National Grid Reference TG 208063).

Type section. The great part of the member is unexposed, so a satisfactory type section cannot be designated.

Reference sections. Small exposures may be found in the vicinity of Cley (TG 054440) and Drayton (TG 175132). Coastal sections at Weybourne Hope show the upper boundary, which is taken at Flint Z of Peake and Hancock (1970, fig. 5, p. 339D–E; Text-fig. 1 herein).

Thickness. Approximately 15 m (Peake and Hancock 1970, fig. 3).

Lithology. Soft chalk with irregularly scattered flints, sometimes forming 'open' bands.



TEXT-FIG. 1. Geological sketch showing the Upper Campanian-Lower Maastrichtian localities and sections of Norfolk described in this paper. The map and the letter key to individual beds are modified from Peake and Hancock (1970).

Boundaries. The member overlies the 'Basal *mucronata* chalk', but the boundary to this unit is ill-defined and possibly mainly based on palaeontological criteria. The latter unit may thus in the future be included in the Eaton Chalk Member. The member is overlain by the Weybourne Chalk Member, the base of which is taken at the top of the sponge-bed hardground above Flint Z of Peake and Hancock (1970, fig. 5).

Distribution. The member is presently only recognized in Norfolk (Peake and Hancock 1970, pl. 2), although probably present at Studland and the Isle of Wight (J. M. Hancock, written communication, June 1986).

Geological age. The member is probably contemporaneous with the lower part of the Ballintoy Chalk Member of Northern Ireland which corresponds to the lower Upper Campanian *basiplana* – *spiniger* Zone of northwest Germany (Fletcher and Wood 1978; Schulz 1985). This level was chosen as stratotype for the neotype of *Belemnitella mucronata mucronata*, and falls within the *Hoplitoplacenticeras* 'vari' Zone of the international ammonite zonal scheme (Christensen *et al.* 1975).

Samples. One sample was collected from an excavation for a house foundation in Cley.

Weybourne Chalk Member

Name. After the village of Weybourne (TG 110430), situated 700 m south of the coastal outcrops of the member.

Type section. The member is exposed in an interrupted line of low chalk bluffs on the north coast of Norfolk at Weybourne Hope. A composite section is shown in Peake and Hancock (1970, fig. 5; Text-fig. 1 herein).

Reference sections. The lower part of the section at Catton Grove (TG 229109) (Peake and Hancock 1970, fig. 6), Keswick (TG 212048), and a former section at Stoke Holy Cross (TG 235016; Text-fig. 1).

Thickness. Approximately 25 m (Peake and Hancock 1970, fig. 3).

Lithology. Chalk with bands of nodular flint, strong and more or less continuous in the lower part. Fossils have a pinkish tinge in the middle 15 m of this unit.

Boundaries. This member overlies Eaton Chalk, the base taken at the top of the sponge-bed hardground above Flint Z of Peake and Hancock (1970, fig. 5) in the section at Weybourne Hope. The upper boundary is drawn at the top of hardground forming the top of the Catton Sponge Bed.

Distribution. The member has only been recognized in Norfolk (Peake and Hancock 1970, pl. 2).

Geological age. Highest part of the lower Upper Campanian, approximately corresponding to the German *roemeri* Zone (Schulz 1985).

Samples. Four samples from Catton Grove, one from Keswick, and one from Stoke Holy Cross (Text-figs 1 and 3).

Catton Sponge Bed

Name. After Catton Grove (TG 229109) in the northern outskirts of Norwich.

Type section. Catton Grove (Peake and Hancock 1970, fig. 6; Text-fig. 1 herein).

Reference sections. Stoke Holy Cross. Foreshore at Sheringham, north coast of Norfolk (see Peake and Hancock 1970, p. 317).

Thickness. From about 0.3 m to a few metres.

Lithology. The member comprises one to three yellow-stained hardgrounds and the intervening soft chalk with bands of often huge flint nodules. The member contains a characteristic 'hardground preservation fauna' comprising casts of originally aragonite shelled bivalves, gastropods and ammonites.

Boundaries. The Catton Sponge Bed forms the top unit of the Weybourne Chalk Member. The lower boundary is placed at the base of the sponge-bed (B in Peake and Hancock 1970, fig. 6) overlying the unlithified Weybourne Chalk Member, while the upper boundary is placed at the top of the hardground which is overlain by the unlithified Beeston Chalk Member. This definition conforms with that of Wood (1988).

Distribution. The member is only known from Norfolk.

Geological age. Boundary between lower and upper Upper Campanian, corresponding to the boundary between the German *roemeri* and *polyplacum* Zones (Schulz 1985). A contemporaneous hardground sequence has been described from the Glenarm Chalk Member of Northern Ireland as the North Antrim Hardground

(Fletcher and Wood 1978). Many of the Norfolk specimens of *B. polyplacum* probably come from this member (J. M. Hancock, written communication, June 1986).

Samples. Two samples from Catton Grove (Text-figs 1 and 3).

Beeston Chalk Member

Name. After Beeston Hill, east of Sheringham on the north coast of Norfolk.

Type section. Caistor St Edmunds (TG 238046) (Peake and Hancock 1970, fig. 6; Text-fig. 1 herein).

Reference section. Stoke Holy Cross (TG 235016).

Thickness. Approximately 25 m (Peake and Hancock 1970, fig. 3).

Lithology. White chalk characterized by irregular bands of large flints many of which appear as flint circles 0.5–3 m or more in diameter when seen on bedding planes. Sometimes two or more circles are concentric, and there may be a hollow core of the trace fossil *Bathichnus paramoudrae* at the centre (Peake and Hancock 1970, pp. 318, 339f; Bromley *et al.* 1975).

Boundaries. The member overlies the highest hardground of the Catton Sponge Bed (Weybourne Chalk Member) and is overlain by the poorly exposed Paramoudra Chalk Member. The upper boundary of the member is defined at the top of a hardground which appears on the shore about 200 metres east of West Runton (Peake and Hancock 1970, p. 339f).

Distribution. The Beeston Chalk Member has only been recorded from Norfolk (Peake and Hancock 1970, pl. 2).

Geological age. Lower part of the upper Upper Campanian roughly equivalent to the German *polyplacum* and *langei* Zones (Schulz 1985). It correlates well with the Portrush Chalk Member of Northern Ireland (Fletcher and Wood 1978).

Samples. Two samples from Caistor St Edmunds and one from Stoke Holy Cross (Text-figs 1 and 3).

Paramoudra Chalk Member

Name. After the name applied to the barrel-shaped flints which are characteristic of the unit (Peake and Hancock 1970, p. 318; Bromley *et al.* 1975). The name thus does not meet the strict demands of a lithostratigraphic term, but since it refers to the lithology and as it has no biostratigraphic connotations there is no strong reason to abandon it.

Reference sections. The member is very poorly exposed and a type section cannot be proposed. Whitlingham (TG 267078), Frettenham (TG 246173) and Postwick (TG 270080) may serve as reference sections. The reference section at Bramerton is no longer exposed (J. M. Hancock, written communication, June 1986).

Thickness. Approximately 25 m (Peake and Hancock 1970, fig. 3).

Lithology. White chalk with repeated hardgrounds and characterized by the occurrence of 'paramoudras'. A 'paramoudra' is a vertically orientated barrel-shaped or cylindrical flint with a semi-lithified core of chalk through which passes a vertical dark tube like burrow which may extend upwards and downwards for many metres. The burrow and the associated 'paramoudra' were described in detail by Bromley *et al.* (1975) who named the trace fossil *Bathichnus paramoudrae*.

Boundaries. The base of the member is defined at the top of a hardground, which crops out on the shore about 200 m east of West Runton (Peake and Hancock 1970, p. 339f).

The upper boundary cannot be precisely defined, as younger beds are only exposed in glacially disturbed masses. The overlying 'pre-*Porosphaera* Beds' of Wood (1967) comprise relatively hard, sometimes yellowish chalk largely without 'paramoudras'. According to J. M. Hancock (pers. comm. 1988) there is a marker bed – the Overstrand Pyramidata hardground – below the Overstrand Hotel Lower Mass and above undoubted chalk with paramoudras. The top of this hardground may serve as the upper boundary of the member.

Distribution. The member is not known outside Norfolk (Peake and Hancock 1970, pl. 2).

Geological age. The member represents the highest Campanian of Norfolk. It is equivalent to the Ballymagarry Chalk Member of Northern Ireland (Fletcher and Wood 1978), and corresponds to the German *grimmensis-granulosus* Zone and perhaps the basal *lanceolata* Zone of Schulz (1978, 1979, 1985).

Samples. One from Whitlingham at the level of the top flint, probably of uppermost Campanian age.

Sidestrand Chalk Member

History. The member encompasses the 'pre-*Porosphaera* Beds' of Wood (1967) and the '*Porosphaera* Beds' of Brydone (1906, 1908, 1938) (see also Peake and Hancock 1970).

Name. After the village of Sidestrand on the northeast coast of Norfolk.

Type section. The sequence exposed in the glacially induced anticlines at Sidestrand (TG 255404) (Text-fig. 1; see also Peake and Hancock 1970, figs 7 and 8). The eastern (left) anticline especially shows a good section through the main part of the member, which comprises the chalk containing flints X to P in the composite section of Peake and Hancock (1970, fig. 7).

Reference sections. Overstrand Hotel Upper Mass (TG 255406).

Thickness. Probably about 10–12 m.

Lithology. White, in places nodular chalk with grey lenticular streaks representing burrows, and about 15 bands of nodular flint. Flint band S is particularly characteristic as it comprises huge cylindrical, black nodules (up to 30 cm thick and 1 m in diameter) with chalk filled holes.

Boundaries. The lower boundary with the Paramoudra Chalk Member is conventionally placed at the top of the Overstrand Pyramidata hardground. The upper boundary is defined at the top of the hardground labelled O in Peake and Hancock (1970, fig. 7).

Distribution. The member has only been recognized along the northeast coast of Norfolk (Peake and Hancock 1970).

Geological age. Lowermost Maastrichtian (Wood 1967). Schulz (1978) referred the Overstrand Hotel Upper Mass to the *lanceolata* Zone, and the part of the member exposed at Sidestrand to the *pseudobtusa* and *obtusa* Zones.

Samples. One sample from Overstrand Hotel Lower Mass, one sample from Bramerton, six samples from Overstrand Hotel Upper Mass and six samples from Sidestrand (Text-figs 1 and 3).

Trimingham Sponge Beds Member

History. The member corresponds to the 'Sponge Beds' of Brydone (1908).

Name. After the village of Trimingham on the northeast coast of Norfolk.

Type section. Trimingham, where the top is occasionally exposed (Peake and Hancock 1970, fig. 7, beds D to G). The lower beds can also be seen at Sidestrand.

Thickness. 2.9 m.

Lithology. Lithified chalk with several erosion surfaces with green-coated pebbles. The chalk is yellow in outcrop, but grey on fresh surfaces. Impressions of large masses of lithistid and hexactinellid sponges are characteristic. Masses of pyrite are not infrequent (Peake and Hancock 1970). Four bands of nodular flint with thick white cortices (K, J, I, H) occur in the upper part of the member.

Boundaries. The lower boundary of the Trimingham Sponge Beds Member is placed at the top of the sponge-bed labelled O in Peake and Hancock (1970, fig. 7). The upper boundary is defined by the top of the thick 'greasy' marl band labelled G in Peake and Hancock (1970, fig. 7).

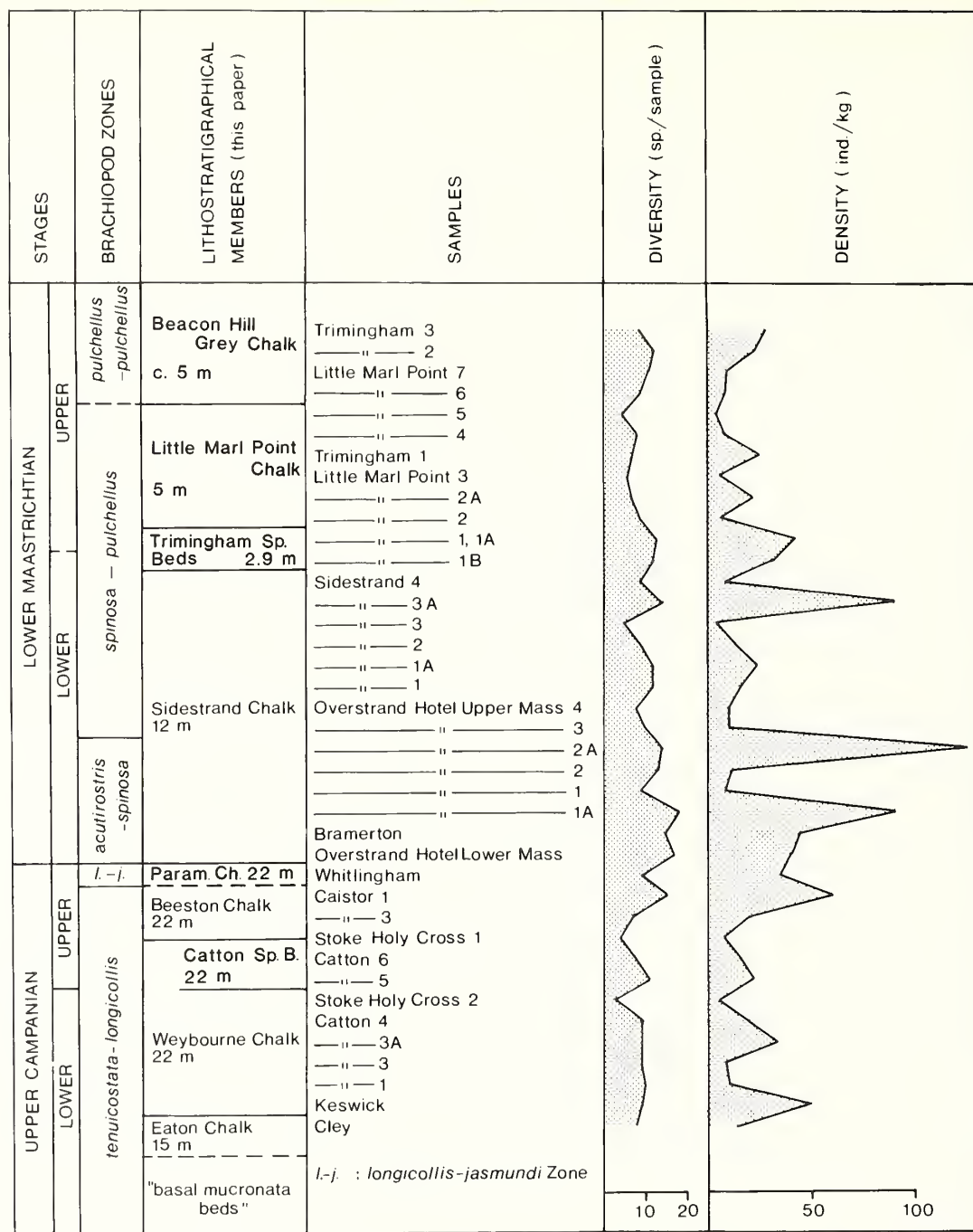
Distribution. Only recorded in the coastal sections of the northeast Norfolk (Peake and Hancock 1970).

Geological age. Top of the lower Lower Maastrichtian. The member probably mainly belongs to the *obtusa* Zone of Schulz (1978, 1985).

Samples. Three samples from the top of the member at Little Marl Point.

Little Marl Point Chalk Member

History. The member comprises the so-called 'White Chalk without *Ostrea lunata*' and the overlying 'White Chalk with *Ostrea lunata*' (Brydone 1906; Peake and Hancock 1970). *Ostrea lunata* was originally proposed as zonal index fossil for the whole of the Maastrichtian exposed at Trimingham. Brydone (1906) demonstrated that *O. lunata* did not occur throughout the sequence and suggested that *Terebratulina gracilis* should take its place as index fossil. Brydone (1906, 1938) suspected that several horizons with *O. lunata* were present, but Peake and Hancock (1970) demonstrated that there is only one horizon with *O. lunata*.



TEXT-FIG. 3. Lithostratigraphy, biostratigraphy, and brachiopod diversity and density of the Norfolk sections.

Name. After the bluff Little Marl Point (TG 298380) on the coast east of Trimingham (Peake and Hancock 1970, fig. 9) where the member is well exposed.

Type section. Little Marl Point (Text-fig. 1; Peake and Hancock 1970, fig. 7, sequence with beds F to B).

Thickness. About 5–5.6 m (Peake and Hancock 1970).

Lithology. Soft white chalk with four horizons (F, D, C, B) of nodular flint and two thin marl bands (below F, E). The top contains a horizon densely packed with the dark blue grey shells of the small oyster *Ostrea lunata*.

Boundaries. The base of the member is placed at the top of the 'greasy' marl band labelled G in Peake and Hancock (1970, fig. 7). The upper boundary is placed at the base of the first soft grey chalk beds of the Beacon Hill Grey Chalk Member labelled A by Peake and Hancock (1970, fig. 7).

Distribution. The member is only known from northeast Norfolk.

Geological age. Lower part of the upper Lower Maastrichtian. Schulz (1979, 1985) correlated it with the *sumensis* Zone of Germany.

Samples. Five samples from Little Marl Point and one from Trimingham mass C of Brydone (1908) (Text-figs 1 and 3).

Beacon Hill Grey Chalk Member

History. The member corresponds to the 'Grey Beds' of Brydone (1906, 1908) and Peake and Hancock (1970).

Name. After Beacon Hill (TG 289383) on top of the cliff overlooking the type locality.

Type section. Trimingham Mass C (Peake and Hancock 1970, figs 7 and 9). The sequence is only occasionally exposed and the fragmentary section figured by Peake and Hancock (1961, fig. 7) was based on a fortuitous exposure opposite Beacon Hill (Peake and Hancock 1970, p. 339H) (approximately TG 292386). Their data have been integrated in the synthetic section shown in Text-figures 1 and 3.

Thickness. About 5 m, but the upper limit is not known (Peake and Hancock 1970, p. 339H).

Lithology. Grey chalk with five flint bands. A fawn-coloured calcarenite 0.1 m thick occurs below the second flint band from the top (Peake and Hancock 1970, p. 339H).

Boundaries. The lower boundary of the member is defined by the base of the first soft grey chalk bed labelled A by Peake and Hancock (1970, fig. 7). The upper boundary is not known since the member comprises the youngest Cretaceous rocks exposed in England.

Distribution. Only known from northeast Norfolk.

Geological age. Lower part of the upper Lower Maastrichtian. The unit belongs to the upper part of the German *sumensis* Zone (Schulz 1978, 1985). A highly characteristic form of *Echinocorys* occurs above the calcarenite band and can be matched exactly in a section near 'die Zeven Wegen' in southern Limburg (Netherlands), where it accompanies *B. sumensis* (N. B. Peake, written communication, June 1986).

Samples. Two samples from Trimingham Mass C, and one sample from Little Marl Point (Text-figs 1 and 3).

BRACHIOPOD STRATIGRAPHY

The Upper Campanian and Maastrichtian Chalk of Norfolk is exposed in small quarries, road cuts, and strongly disturbed coastal cliff sections. The majority of the sections are only a few metres thick. The succession is furthermore characterized by hardgrounds reflecting periods of non-deposition and perhaps erosion. It is thus clear that a chart showing the full range of brachiopod species through the time interval represented by the investigated sequence cannot be constructed. Exposure of the Campanian–Maastrichtian boundary strata are particularly fragmentary.

The Chalk of Norfolk is thus here dated within the framework of the brachiopod zonation worked out for the thick continuous Campanian–Maastrichtian boundary section at Krons Moor, northwest Germany (Surlyk 1982, 1984). Schulz (1978, 1979, 1985) presented a detailed belemnite zonation for the Krons Moor sequence and this zonation is well integrated with the brachiopod zonation. It is thus possible to use the combined evidence from brachiopods and belemnites in the correlation of the Norfolk sequence.

The localities of Text-figure 1 were first arranged in ascending stratigraphic order on the basis of evidence from macrofossils, notably belemnites and to some extent echinoids (Schulz 1978, 1979, 1985; Peake and Hancock 1970; Wood 1967) and field mapping (Peake and Hancock 1970) supplemented by scattered information in the literature on the Cretaceous of the British Isles (Fletcher and Wood 1978).

The brachiopod species were then plotted on this scheme and their vertical distributions compared with ranges in the Krons Moor section (Surlyk 1982, 1984) and to more limited successions in Denmark (Surlyk 1984) and Poland (Bitner and Pisera 1979).

Seven brachiopod zones were recognized in the Krons Moor section within the interval represented by the *langei* through *sumensis* belemnite zones (Text-fig. 3). The Maastrichtian portion of the Norfolk and Krons Moor sequences can be roughly correlated, while the Norfolk Campanian investigated here reaches lower than the part exposed in Krons Moor.

It is important to stress that both the brachiopod and belemnite zones are defined by first or last occurrences of species with Krons Moor as the key locality. This means, for example, that a slightly later appearance of a brachiopod index species in Norfolk relative to a belemnite index species is reflected by an upwards shift of a brachiopod zone boundary in respect to the belemnite zone boundary. Schemes showing the correlation of the same brachiopod and belemnite zones in northwest Germany and Norfolk respectively are thus somewhat different. This is shown in Text-figure 4.

The brachiopod zones are defined and named following the system proposed by Murphy (1977). The lower boundary of each zone is defined in a stratotype by a biostratigraphic event such as the first appearance or last occurrence of a species. The upper boundary is defined by the base of the next, higher zone to avoid gaps or overlap of zones. A binomial nomenclature is used to name the zone. The name of the species which defines the lower boundary is followed by the name of the species which defines the lower boundary of the following zone. Thus the *longicollis-jasmundi* Zone is from the first occurrence of *Terebratulina longicollis* to immediately below the first occurrence of *Gisilina jasmundi*. The following *jasmundi-acutirostris* Zone is defined by the first occurrences of *Gisilina jasmundi* and *Rugia acutirostris* respectively.

Most of the brachiopod zones recognized in Krons Moor are also represented in Norfolk. The *tenuicostata-longicollis* Zone includes the localities Cley, Stoke Holy Cross, Catton and Caistor (Text-fig. 2). This zone can undoubtedly be subdivided, when the brachiopod faunas from continuous sections through the lower Upper Campanian are investigated.

The *longicollis-jasmundi* Zone corresponds to the highest Campanian in Krons Moor and seems to be represented by the Whitlingham locality.

The basal Maastrichtian *jasmundi-acutirostris* Zone in Krons Moor is defined by the first occurrence of *Gisilina jasmundi* and *Rugia acutirostris*. *G. jasmundi* has its first occurrence in Krons Moor sample F10 which was sampled 20 cm below flint band F600. The lowest *Belemnella lanceolata*, which defines the base of the Maastrichtian (e.g. Schulz 1978, 1979), was found at the level of F600. This means that the bases of the *lanceolata* Zone and the *jasmundi-acutirostris* Zone essentially coincide. For convenience, Schulz (1978), however, placed the Campanian-Maastrichtian boundary precisely at the midpoint of F600. The *jasmundi-acutirostris* Zone thus seems to have its base immediately below the Campanian-Maastrichtian boundary (Surlyk 1982, fig. 1), but this only reflects the greater precision of sample localization in respect to the lithological marker beds. *G. jasmundi* and *R. acutirostris* occur for the first time in the Norfolk material in Overstrand Hotel Lower Mass which is the next locality stratigraphically above Whitlingham (Text-fig. 2). It is thus highly probable that the *jasmundi-acutirostris* Zone is represented by unexposed strata stratigraphically between Whitlingham and Overstrand Hotel Lower Mass.

The *acutirostris-spinosa* Zone is defined by the first occurrence of *Rugia acutirostris* and the last occurrence of *Rugia spinosa*. In Norfolk it is represented by the localities Overstrand Hotel Lower Mass, Bramerton, and Overstrand Hotel Upper Mass samples 1-2A (Text-fig. 2).

The *spinosa-subtilis* Zone is defined by the last occurrence of *Rugia spinosa* and the first occurrence of *Terebratulina subtilis*. The latter species has a much longer vertical range in Norfolk

Thickness in Kronsmoor	STAGES			BELEMNITE/ ECHINOID ZONES	BRACHIOPOD ZONES	
					Kronsmoor	Norfolk
50	MAASTRICHTIAN	LOWER	upper	<i>B. sumensis</i>	<i>pulchellus-pulchellus</i>	<i>pulchellus-pulchellus</i>
40						
30			lower		<i>subtilis-pulchellus</i>	<i>spinosa-pulchellus</i>
20				<i>B. obtusa</i>	<i>spinosa-subtilis</i>	
10				<i>B. pseud- obtusa</i>	<i>acutirostris-spinosa</i>	<i>acutirostris-spinosa</i>
0	CAMPANIAN	UPPER	upper	<i>B. lanceo- lata</i>	<i>jasmundi-acutirostris</i>	?
10			upper	<i>M. grimmensis - C. granulosis</i>	<i>longicollis-jasmundi</i>	<i>longicollis-jasmundi</i>
20				<i>Bt. langei</i>	<i>tenuicostata-longicollis</i>	<i>tenuicostata-longicollis</i>
30						
40						
m						

TEXT-FIG. 4. Scheme showing the correlation of the belemnite and brachiopod zones of Kronsmoor (northwest Germany) and Norfolk based on Schulz (1978, 1979, 1985), Surlyk (1982, 1984) and this paper.

than in northwest Europe generally (Text-fig. 2) and its first appearance is thus of no value in regional correlation. The next higher stratigraphic event used in the northwest European brachiopod zonation is the incoming of *Trigonosemus pulchellus*. This species has not been found in our material but is reported from the Grey Beds (the Beacon Hill Grey Chalk Member of this paper) by Wood (1967). This is confirmed by the study of the museum collections of the British Geological Survey by one of us (F.S.). The Beacon Hill Grey Chalk Member includes the samples Little Marl Point 6 and Trimmingham 2 and 3.

The lowest occurrence of *T. pulchellus* is not known, but is provisionally taken to correspond to the base of the Beacon Hill Grey Chalk Member. A *spinosa-pulchellus* Zone can thus be recognized as including the localities Overstrand Hotel Upper Mass 3 and 4, Sidestrand, Little Marl Point 1–5, and Trimmingham 1.

It is followed by the *pulchellus-pulchellus* Zone defined by the first and last appearance of *Trigonosemus pulchellus*. The top of the zone may not be exposed in Norfolk.

SYSTEMATIC PALAEOLOGY

Repositories. Specimens from Norfolk have MGUH as prefix to their registration numbers. MGUH refers to the formal numbering system of Geological Museum, the University of Copenhagen, Denmark. Specimens from Lägerdorf and Krons Moor are prefixed SPGIH, referring to the formal numbering system of the Institute of Geology and Palaeontology, the University and Museum of Hamburg, Germany. The abbreviation in the plate captions WKC refers to specimens collected by Walter Kegel Christensen, Geological Museum, the University of Copenhagen.

Family LINGULIDAE Menke, 1828

Genus LINGULA Bruguiere, 1797

Type species. *Lingula anatina* Lamarck, 1801, p. 141.

Lingula cretacea? Lundgren, 1885

Plate 1, figs 1 and 2

- 1885 *Lingula cretacea* Lundgren, p. 20, pl. 1, fig. 1.
- 1894 *Lingula cretacea* Lundgren; Posselt, p. 14.
- 1909 *Lingula cretacea* Lundgren; Nielsen, p. 17.
- 1972 *Lingula cretacea* Lundgren; Surlyk, p. 27, figs 5 and 12.
- 1982 *Lingula cretacea* Lundgren; Surlyk, fig. 1.

Material. The shell of this species is very fragile, and when found in the washed residues is highly fragmented. The Norfolk material consists of one dorsal and one ventral valve, and twenty-five fragments. Significant measurements have not been obtained. Catalogue numbers MGUH 16841, 16842.

EXPLANATION OF PLATE 1

- Figs 1 and 2. *Lingula cretacea?* Lundgren, 1885. 1, MGUH 16841, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 2A, Norfolk; interior-posterior view of ventral valve, $\times 35$. 2, MGUH 16842, lower Lower Maastrichtian, Little Marl Point 1B, Norfolk; exterior of broken valve, $\times 30$.
- Figs 3 and 4. *Isocrania costata* (J. de C. Sowerby, 1823). 3, MGUH 16843, upper Lower Maastrichtian, Trimmingham (coll. WKC, 1971), Norfolk; interior of adult ventral valve, $\times 12$. 4, MGUH 16844, lower Lower Maastrichtian, Sidestrand 1, Norfolk; exterior of juvenile ventral valve showing stem-shaped attachment surface, $\times 27$.
- Figs 5 and 6. *Craniscus* sp. MGUH 16845, lower Lower Maastrichtian, Little Marl Point 1A, Norfolk. 5, interior of fragmented dorsal valve, $\times 50$. 6, oblique lateral view showing median septum, $\times 50$.
- Fig. 7. *Lacazella (Bifolium) wetherelli* Morris, 1851, MGUH 16846, lower Lower Maastrichtian, Little Marl Point 1B, Norfolk; interior of adult ventral valve, $\times 10$.



Description. Shell small and thin. Outline irregular elongate, oval, almost parallel-sided, gently biconvex. Beak of ventral valve contains broad triangular groove for passage of pedicle. Posterior margins of shell are broadly pointed, anterior margins broadly rounded. Shell surface smooth apart from numerous growth lines. Shell composed of a brown to whitish material. Interior details not seen.

Remarks. The material is too sparse and fragmented to give a more precise statement of the species than *Lingula cretacea*?

Occurrence. Catton 1 and 3A, Bramerton, Overstrand Hotel Upper Mass 2A, Sidestrand 3A, Little Marl Point 1B and 2A and Trimingham 2?

Family CRANIIDAE Menke, 1828

Genus CRANIA Retzius, 1781

Type species. *Anomia craniolaris* Linnaeus, 1758, p. 700.

Crania aff. *craniolaris* (Linnaeus, 1758)

1972 *Crania* aff. *craniolaris* (Linnaeus); Surlyk, p. 27, fig. 5.

Material. Only one fragmented ventral valve, estimated length 4.4 mm.

Description. Outline rounded; valve attached to substrate by entire outer surface. Margin thickened and pustulose forming rather wide limbus. Anterior and posterior adductor scars close together in posterior part of valve. Surface of attachment area shows prominent growth lines and very fine radial striation, which may reflect nature of substrate.

Remarks. The specimen is too fragmentary for a reliable species determination, but it belongs to a fairly common group of rather small craniaceans, which occur in the chalk of northwest Europe and which resemble *Crania craniolaris* (Linnaeus 1758, p. 700) in virtually all features except for their much smaller size.

Occurrences. Trimingham 1 and elsewhere in the Upper Campanian and Maastrichtian of northwest Europe.

Genus ISOCRANIA Jaekel, 1902

Type species. *Crania egnabergensis* Retzius, 1781, p. 52.

Isocrania costata (J. de C. Sowerby, 1823)

Plate 1, figs 3 and 4

- 1823 *Crania costata* J. de C. Sowerby, pl. 35, fig. 6.
- 1973 *Isocrania costata* (J. de C. Sowerby); Surlyk, figs 1, 2, 5–10, 12; pl. 1, figs 1–11, 16–19; pls 3, 4, 6; fig. 12.
- 1975 *Isocrania costata* (J. de C. Sowerby); Nestler, p. 42, text-fig. 52.
- 1979 *Isocrania costata* (J. de C. Sowerby); Bitner and Pisera, p. 70, fig. 2.
- 1982 *Isocrania costata* (J. de C. Sowerby); Surlyk, fig. 1.
- 1984 *Isocrania costata* (J. de C. Sowerby); Ernst, p. 65–67, pl. 6, figs 3 and 4; pl. 7, figs 1–6; pl. 8, figs 1, 2, 9–11.
- 1984 *Isocrania costata* (J. de C. Sowerby); Surlyk and Johansen, fig. 1.
- 1987a *Isocrania costata* (J. de C. Sowerby); Johansen, fig. 7.
- 1988 *Isocrania costata* (J. de C. Sowerby); Johansen, fig. 2, pl. 4, fig. 4.

Material. Three dorsal, thirteen ventral valves and seven fragments; largest specimens all somewhat fragmentary. Dorsal valve from Sidestrand 1 is 5.8 mm wide. Catalogue numbers MGUH 16843, 16844.

Description. Outline rectangular to circular. Dorsal valve low conical with sculpture of 10–30 primary ribs. A few additional ribs form by intercalation increasing to a total of about 35. Ribs are strong, prominent, protruding somewhat beyond the valve margin. Anterior and posterior ribs straight; lateral ribs curve slightly in posterior direction. Surface of valve between ribs covered with coarse, radially directed spines. Interior surface has two closely situated anterior adductor scars. Posterior adductors separated by septum-like extension of limbus and also limited antero-laterally by such extensions. Limbus wide and finely pustulose. Ventral valve similar to dorsal valve in outline and sculpture except for flat protegular node in some cases showing imprints of tiny attachment substrates. Anterior adductor scars drop-shaped, converging anteriorly towards midline of valve. Posterior adductor scars oval, of same size and in same position as in dorsal valve. A pointed septum is situated between anterior adductors.

Remarks. *I. costata* can be distinguished from earlier forms known from the English Chalk by the low number of ribs which only protrude slightly beyond the valve margin, and by the subcentral position of the umbo.

Occurrence. Cley, Catton 5, Overstrand Hotel Lower Mass, Sidestrand 1, 1A and 3A, Little Marl Point 1B, 1, 1A, 2 and 4, and Trimingham 2. In addition the species is recorded from the Upper Campanian and Maastrichtian of northern Germany and eastern Poland, and from the Maastrichtian and Lower Danian of Denmark.

Genus CRANISCUS Dall, 1871

Type species. *Crania tripartita* Münster, 1837, p. 297.

Craniscus sp.

Plate 1, figs 5 and 6

Material. Three fragmentary dorsal valves. Largest valve 3.6 mm in diameter, and from Bramerton sample. Catalogue number MGUH 16845.

Description. Outline irregular subrectangular to subrounded. Dorsal valve conical, surface smooth. Anterior adductor scars in dorsal valve situated on two strong ridges extending postero-laterally from apex, united with the median septum or ridge. The three ridges divide the valve into three chambers. Margins of valve not thickened. Inner surface with densely spaced minute cavities.

Remarks. The material is too poorly preserved to warrant any specific determination; generic assignment is based on the three characteristic ridges dividing the dorsal valve into three compartments.

Occurrence. Bramerton and Little Marl Point 1A.

Order RHYNCHONELLIDA Kuhn, 1949 Family RHYNCHONELLIDAE Gray, 1848 Unidentified rhynchonellids

Material. Twenty-two dorsal, forty-nine ventral valves and more than two hundred and fifty fragments. The material is too fragmentary for any further description but belongs to the family Rhynchonellidae, showing the characteristic glossy, fibrous structure of the thick and impunctate shell. Some fragments probably belong to *Cretirhynchia* sp. described below.

Occurrence. Cley, Keswick, Catton 3A and 4, Stoke Holy Cross 2, Catton 5 and 6, Caistor 1, Whitlingham, Bramerton, Overstrand Hotel Upper Mass 1A and 2, Sidestrand 1A and 2, Little Marl Point 1B, 1, 1A and 2, Trimingham 1, Little Marl Point 6 and 7, and Trimingham 2 and 3.

Subfamily CYCLOTHYRIDINAE Makridin, 1955
Genus CRETIRHYNCHIA Pettitt, 1950

Type species. Terebratulula plicatilis J. Sowerby, 1816, p. 37.

Cretirhynchia sp.

Plate 2, figs 1 and 2

Material. Eight complete shells, nine dorsal and twelve ventral valves and a large number of fragments. All specimens represent early juvenile stages and no measurements have been obtained. Catalogue numbers MGUH 16847, 16848.

Description. Shell smooth, pointed oval in juvenile stages. Beak suberect to erect; deltidial plates have a characteristic growth pattern which results in two laterally directed wing-like doublings of the plates. This pattern is a result of changes in growth direction of deltidial plates during ontogeny as described by Steinich (1965). Material does not allow adequate description of brachidium or hinge, although inner socket ridges are strong, low, short and converge strongly anteriorly. Posteriorly they almost meet. Crura strongly built, long, converging ventrally.

Remarks. A large number of species of *Cretirhynchia* are recorded from the Upper Campanian and Lower Maastrichtian of Norfolk (e.g. Peake and Hancock 1961, 1970; Pettitt 1950, 1953). From the Upper Campanian *C. lentiformis* (Woodward) of the 'limbata series' is present below the Weybourne Chalk Member, and *C. arcuata* Pettitt of the 'plicatilis series' above this member. *C. norvicensis* Pettitt and *C. woodwardi* (Davidson) appear at the base of the Weybourne Chalk Member. In the Lower Maastrichtian *C. magna* Pettitt occurs in the Sidestrand Chalk Member along with *C. aff. arcuata* Pettitt and *C. retracta* (Roemer). *C. limbata* s.s. (Schlotheim) appears in the upper Lower Maastrichtian Beacon Hill Grey Chalk Member. Note that Pettitt's (1950, 1953) species are in need of revision.

It is not at present possible to recognize juveniles of these species and thus not possible to assign the present material to any known species.

Occurrence. Catton 1 and 3, Caistor 1 and 3, Overstrand Hotel Lower Mass, Bramerton, Overstrand Hotel Upper Mass 2A, Sidestrand 1 and 3A, Little Marl Point 1B, 2A, 5 and 7, and Trimmingham 2 and 3.

Cretirhynchia limbata (Schlotheim, 1813)

Plate 2, figs 3–5

(1798) *Térébratulus fossiles* Faujas, pl. 26, fig. 4.

1813 *Terebratulites limbatus* Schlotheim, p. 113.

EXPLANATION OF PLATE 2

Figs 1 and 2. *Cretirhynchia* sp., MGUH 16847, lower Lower Maastrichtian, Little Marl Point 1B, Norfolk. 1, juvenile specimen in dorsal view, $\times 20$. 2, MGUH 16848, lower Lower Maastrichtian, Little Marl Point 1A, Norfolk; small juvenile specimen in dorsal view, $\times 35$.

Figs 3–5. *Cretirhynchia limbata* (Schlotheim, 1813), MGUH 16849, upper Upper Campanian, Stoke Holy Cross 1, Norfolk. 3, interior of medium-sized ventral valve, $\times 10$. 4, frontal view showing uniplicate sinus with low rounded costae at anterior shell margin, $\times 10$. 5, lateral view showing convexity of ventral valve and curvature of sinus and rostrum, $\times 8$.

Figs 6 and 7. *Carneithyrus subcardinalis* (Sahni, 1925). 6, MGUH 16850, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 2A, Norfolk; juvenile specimen in dorsal view, $\times 10$. 7, MGUH 16851, upper Lower Maastrichtian, Little Marl Point 6, Norfolk; posterior part of adult dorsal valve showing fused cardinalia, $\times 10$.



- 1841 *Terebratula subplicata* Mantell; Roemer, p. 38, fig. 10.
 1856 *Rhynchonella limbata* (Schlotheim); Boll, p. 47.
 1894 *Rhynchonella limbata* (Schlotheim); Posselt, p. 27, fig. 1; pl. 2, fig. 16.
 1953 *Cretirhynchia limbata* (Schlotheim); Pettitt, p. 27, fig. 16; pl. 1, fig. 1a-c; pl. 2, fig. 12a-c; text-figs 7a-c, 8, 9.
 1965 *Cretirhynchia limbata* (Schlotheim); Steinich, p. 24, fig. 13; pl. 2, fig. 4a-d.
 1972 *Cretirhynchia limbata* (Schlotheim); Surlyk, p. 24, fig. 17.

Material and occurrence. One bivalved, fragmentary adult specimen found in the Upper Campanian sample Stoke Holy Cross 1. Dimensions: length, 11.4 mm; width, 10.9 mm; length of dorsal valve, 10.0 mm; width of hinge line, 2.5 mm; width of foramen, 0.5 mm. Fragments of this species are probably also present among the fragments of the *Cretirhynchia* sp. described elsewhere in this paper. Catalogue number MGUH 16849.

Description. Shell relatively pointed subtriangular in outline. Shell surface smooth except for weak rib pattern developed along anterior shell margin. Uniplicate sinus with low, rounded costae developed in anterior commissure. Shell almost plano-convex with dorsal valve strongly convex. Ventral valve fragmentary but probably only slightly convex. Beak low, pointed incurved; foramen is small, oval to subcircular and limited by collar-like deltidium. Hinge strong, consists of strongly built, blunt, triangular hinge teeth, inner sockets which continue directly into the crura. Cardinal process present but material does not allow study of brachidium.

Remarks. Both external features and nature of the hinge are consistent with descriptions of *Cretirhynchia limbata* (Schlotheim) by Steinich (1965) and others. This is the first record of *C. limbata* in the Upper Campanian of Norfolk. It is widely distributed in the Maastrichtian of England, the Netherlands, northern Germany and Denmark.

Family TEREBRATULIDAE Gray, 1840

Genus CARNEITHYRIS Sahni, 1925

Type species. *Carneithyrus subpentagonalis* Sahni, 1925, p. 364.

Carneithyrus subcardinalis (Sahni, 1925)

Plate 2, figs 6 and 7

- 1842 *Terebratula carnea* J. Sowerby; Hagenow, p. 539, fig. 13.
 1894 *Terebratula carnea* J. Sowerby; Posselt, p. 38, fig. 29.
 1909 *Terebratula carnea* J. Sowerby; Nielsen, p. 163, pl. 2, figs 68-77.
 1925 *Chatwinothyris subcardinalis* Sahni, p. 369, pl. 23, fig. 9; pl. 24, fig. 4, 4a; pl. 26, fig. 4, 4a.
 1929 *Chatwinothyris subcardinalis* Sahni; Sahni, p. 40, pl. 5, figs 20-22; pl. 6, figs 10-12; pl. 10, figs 1-4.
 1965 *Chatwinothyris subcardinalis* Sahni; Steinich, p. 37, figs 24-34; pl. 5, figs 1a-d, 2a-d, 3, 4; pl. 7, figs 1a, b, 2; pl. 11, figs 1, 2a-b, 3.
 1972 *Carneithyrus subcardinalis* (Sahni); Surlyk, p. 24, figs 5, 11, 16-18; pl. 5, fig. c.
 1975 *Carneithyrus subcardinalis* (Sahni); Asgaard, p. 320, pl. 8, figs 1-4.
 1982 *Carneithyrus subcardinalis* (Sahni); Surlyk, fig. 1, pl. 1, fig. a.
 1984 *Carneithyrus subcardinalis* (Sahni); Surlyk and Johansen, fig. 1.
 1987a *Carneithyrus subcardinalis* (Sahni); Johansen, p. 13, pl. 2, fig. 2.
 1988 *Carneithyrus subcardinalis* (Sahni); Johansen, fig. 2.

Material. Five complete shells, ten dorsal, twenty-two ventral valves and about ninety fragments. No usable measurements have been obtained. Catalogue number MGUH 16851.

Description. Adult shell large, relatively thin, with large punctae. The outline changes during ontogeny from elongated pointed oval to oval - subpentagonal. Biconvex except for earliest juvenile stages which are almost plano-convex. Shell surface smooth, anterior commissure straight. Hinge line short; beak changes from acute and suberect to incurved in adult stages. Foramen very small through ontogeny, due to presence of two

characteristically large triangular deltidial plates. In large forms foramen is circular and of submesothyridid to mesothyridid pin-hole type. Hinge strong in adults with dorsal cardinalia so that socket ridges, cardinal process and crural bases are fused. Cardinal process typically lacking. Brachidium simple, consists, in juveniles, of short, rather widely separated crura. During growth descending branches develop from dorsal part of crura, ultimately to fuse and thereby form a transverse bridge.

Remarks. The material is consistent with descriptions of *Carneithyris subcardinalis* (Sahni) by Sahni (1925, 1929), Steinich (1965), Asgaard (1975) and Johansen (1987a). A more detailed description of the ontogenetic stages is given by these authors. The juveniles of *C. subcardinalis* are distinguished from other small smooth-shelled related species by the very small foramen limited by two triangular, deltidial plates.

Occurrence. The species was first described by Sahni (1925) from the Lower Maastrichtian *Ostrea lunata* Zone of Trimingham, Norfolk. In the present paper the species is recorded from the following samples: Catton 1, 3, 5? and 6, Stoke Holy Cross 1, Caistor 1?, Overstrand Hotel Lower Mass, Bramerton, Overstrand Hotel Upper Mass 1A, Sidestrand 1 and 3A, Little Marl Point 1A, 4, 5 and 6, and Trimingham 2 and 3. *Carneithyris subcardinalis* is in addition recorded from the Maastrichtian and Upper Campanian of Denmark, northern Germany and Poland.

Order TEREBRATULIDA Waagen, 1883
Family TEREBRATULIDAE Gray, 1840

Undetermined terebratulid

Remarks. Fragments of a punctate, smooth and thin-shelled form occur in the samples Overstrand Hotel Upper Mass 2, Caistor 3 and 1, all of Early Maastrichtian age. The state of the material does not allow any generic assignment of the fragments but it is clearly a juvenile terebratulid.

Family CANCELLOTHYRIDIDAE Thomson, 1926
Genus TEREBRATULINA d'Orbigny, 1847

Type species. *Anomia craniolaris* Linnaeus, 1758, p. 700.

Terebratulina chrysalis (Schlotheim, 1813)

Plate 3, figs 1–5

- 1813 *Terebratulites chrysalis* Schlotheim, p. 113.
- 1894 *Terebratulina striata* Wahlenberg; Posselt, p. 32, fig. 19; p. 5, footnote 3; p. 10.
- 1909 *Terebratulina striata* Wahlenberg; Nielsen, p. 159, fig. 20; pl. 1, figs 28–32; p. 134, fig. 20; p. 137, fig. 20; pp. 138–139, fig. 20; p. 141, fig. 20; p. 144.
- 1965 *Terebratulina chrysalis* (Schlotheim); Steinich, p. 53, figs 44–61; pl. 8, fig. 1a–d; pl. 9, figs 1–5, 9a, b, 10a, b.
- 1972 *Terebratulina chrysalis* (Schlotheim); Surlyk, p. 21, figs 12–18; pl. 4, figs 5–8.
- 1979 *Terebratulina chrysalis* (Schlotheim); Bitner and Pisera, p. 73, pl. 3, figs 12–15.
- 1982 *Terebratulina chrysalis* (Schlotheim); Surlyk, fig. 1.
- 1984 *Terebratulina chrysalis* (Schlotheim); Surlyk and Johansen, fig. 1.
- 1987a *Terebratulina chrysalis* (Schlotheim); Johansen, p. 14, fig. 14A–D; pl. 4, figs 1–5.
- 1988 *Terebratulina chrysalis* (Schlotheim); Johansen, fig. 2; pl. 2, figs 7–10.

Material. At least forty-five complete shells, one hundred and thirty-five dorsal and seventy ventral valves and a large number of fragments. The size of fully grown specimens has not been measured or estimated. Catalogue numbers MGUH 16852–16855.

Description. Shell relatively large. Outline changes during ontogeny from elongated subtriangular to elongated subpentagonal. The juveniles possess large, well-defined auricles which in adults become small and oblique. Shell surface with 8 to more than 60 straight ribs, increasing by intercalation. Ribs strong and coarsely

tuberculate in the juveniles, sculpture characteristically consists of nodes placed on top of ribs, never forming transverse half rings as is seen in *Terebratulina faujasii* and *T. longicollis*. Rib width constant through ontogeny, interspaces very wide in large specimens. Beak short, suberect; foramen changes from subtriangular hypothyriddid to oval submesothyriddid with growth. Hinge relatively weak. Brachidium development as in other terebratuliniids (e.g. Steinich 1965) forming strong crura; short, robust descending branches terminate in closed brachial ring, rather wide in *T. chrysalis*. The spicular skeleton well-mineralized; plectolophe.

Remarks. The material is consistent with descriptions of *Terebratulina chrysalis* by a large number of authors, e.g. Steinich (1965) and Johansen (1987a). *T. longicollis* Steinich differs from *T. chrysalis* in the lack of intercalated ribs or branching of ribs, the coarse rib sculpture and very elongated outline. *T. faujasii* (Roemer) differs from *T. chrysalis* in possessing single undivided ribs ornamented by coarse transverse half rings.

Occurrence. Cley, Catton 3 and 4, Stoke Holy Cross 2, Caistor 1 and 3, Whitlingham, Overstrand Hotel Lower Mass, Bramerton, Overstrand Hotel Upper Mass 1A, 1, 2, 2A, 3 and 4, Sidestrand 1, 1A, 2, 3, 3A, 4 and 5, Little Marl Point 1B, 1, 1A, 2A, 3, 4 and 7, and Trimingham 2 and 3. *Terebratulina chrysalis* is widespread and very common throughout the Upper Cretaceous and Danian chalks of northwest Europe.

Terebratulina faujasii (Roemer, 1841)

Plate 4, figs 8 and 9

- 1841 *Terebratula faujasii* Roemer, p. 40, fig. 24; pl. 7, fig. 8.
- 1965 *Terebratulina faujasii* (Roemer); Steinich, p. 72, figs 76–94; pl. 9, figs 6–8; pl. 10, figs 1a–d, 2–5.
- 1972 *Terebratulina faujasii* (Roemer); Surlyk, p. 18, figs 5, 12, 14–16, 18; pl. 2, figs c–g.
- 1982 *Terebratulina faujasii* (Roemer); Surlyk, fig. 1, pl. 1, figs c and d.
- 1984 *Terebratulina faujasii* (Roemer); Surlyk and Johansen, fig. 1.
- 1987a *Terebratulina faujasii* (Roemer); Johansen, p. 15, pl. 7, fig. 3.
- 1988 *Terebratulina faujasii* (Roemer); Johansen, fig. 2.

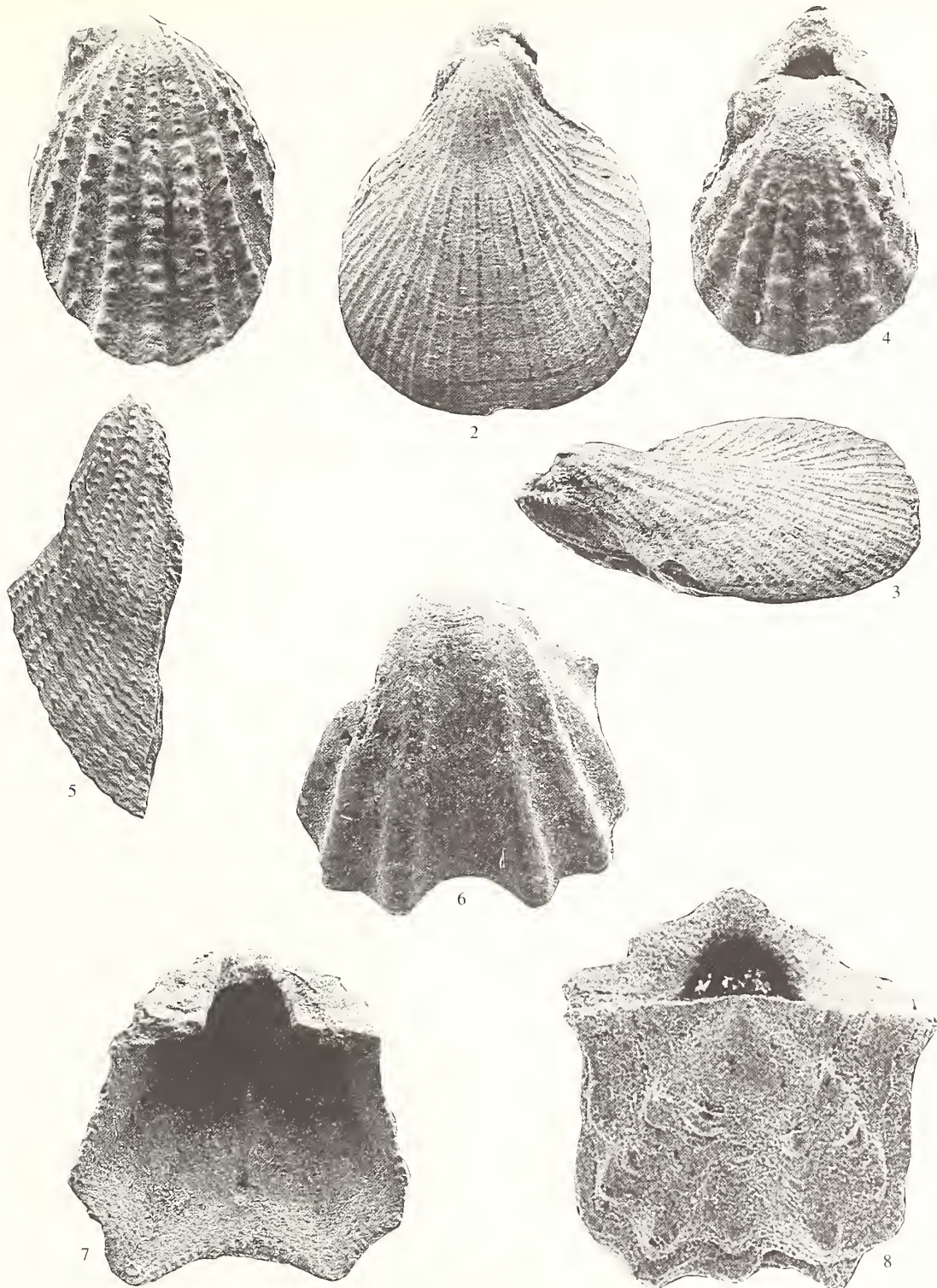
Material. Seventy-five complete shells, 296 dorsal, 268 ventral valves, and approximately 300 fragments. Largest specimen is a fragmented dorsal valve from Sidestrand 3A: length of dorsal valve, 4.5 mm; width, 5.0 mm; 12 ribs. Catalogue numbers MGUH 16861, 16860.

Description. Outline changes during ontogeny from broad subtriangular to elongated subtriangular with maximum width at anterior shell margin. Auricles large. Shell surface with 8–12 straight, coarse, broad single ribs, with sculpture of very coarse prominent transverse half rings on rib crests. Beak low, suberect to erect; foramen large, triangular, submeso- to mesothyriddid in the adults. Brachidium consists of strong crura, distinct descending arms and closed brachial ring. Spicular skeleton well-mineralized; plectolophe.

Remarks. *Terebratulina faujasii* differs from other *Terebratulina* species in possessing single ribs with a sculpture of coarse transverse half rings. Juveniles of *Gisilina jasmundi* Steinich differ from *T.*

EXPLANATION OF PLATE 3

- Figs 1–5. *Terebratulina chrysalis* (Schlotheim, 1813). 1, MGUH 16852, lower Lower Maastrichtian, Sidestrand 1A, Norfolk; exterior of juvenile dorsal valve, $\times 15$. 2 and 3, MGUH 16853, Lower Maastrichtian, Rordal, Denmark (coll. MBJ, 1981); 2, adult specimen in dorsal view, $\times 10$; 3, lateral view. 4, MGUH 16854, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 2A, Norfolk; small juvenile specimen in dorsal view, $\times 35$. 5, MGUH 16855, upper Upper Campanian, Caistor 1, Norfolk; fragment of large specimen showing characteristic rib pattern, $\times 10$.
- Figs 6–8. *Argyrotheca hirundo* (Hagenow, 1842). 6, MGUH 16856, Campanian–Maastrichtian boundary strata?, Bramerton, Norfolk; exterior of adult ventral valve, $\times 22$. 7, MGUH 16857, lowermost Maastrichtian, Bramerton, Norfolk; interior of adult ventral valve, $\times 22$. 8, SPGIH 3534, upper Lower Campanian, G 79, Lägerdorf; adult specimen in dorsal view, $\times 20$.



faujasii in possessing a larger number of weaker sculpted ribs. Juveniles of *T. chrysalis* (Schlotheim) differ from *T. faujasii* in having intercalated ribs at a very early growth stage.

Occurrence. Catton 3A, 4 and 5, Caistor 1, Whitlingham, Bramerton, Overstrand Hotel Lower Mass, Overstrand Hotel Upper Mass 1, 1A, 2, 2A, 3 and 4, Sidestrand 1, 1A, 2, 3, 3A, 4 and 5, Little Marl Point 1, 1A, 1B, 2, 2A and 3, Trimingham 1, Little Marl Point 6 and 7, and Trimingham 2 and 3. In addition, the species is recorded from the Upper Campanian – Maastrichtian of Denmark, northern Germany and Poland.

Terebratulina gracilis (Schlotheim, 1813)

Plate 4, figs 1–7

- 1813 *Terebratulites gracilis* Schlotheim, p. 113, pl. 3, fig. 3a, b.
- 1860 *Terebratulina gracilis* (Schlotheim); Bosquet, p. 390.
- 1866 *Terebratulina gracilis* (Schlotheim); Schloenbach, p. 287, pl. 38, figs 18a, b, 19a, b, 20a, b.
- 1894 *Terebratulina gracilis* (Schlotheim); Posselt, p. 33, fig. 20; pl. 3, figs 5–7.
- 1908 *Terebratulina gracilis* (Schlotheim); Brydone, p. 403.
- 1909 *Terebratulina gracilis* (Schlotheim); Nielsen, p. 161, fig. 22; p. 134, fig. 22; p. 137, fig. 22.
- 1965 *Terebratulina gracilis* (Schlotheim); Steinich, p. 81, figs 95–114; pl. 11, fig. 1a–d; pl. 12, figs 1, 2a, b; pl. 13, figs 1–3.
- 1972 *Terebratulina gracilis* (Schlotheim); Surlyk, p. 24, figs 5, 9, 11, 13, 15b, 18–22.
- 1982 *Terebratulina gracilis* (Schlotheim); Surlyk, fig. 1.
- 1984 *Terebratulina gracilis* (Schlotheim); Surlyk and Johansen, fig. 1.
- 1987a *Terebratulina gracilis* (Schlotheim); Johansen, p. 16, pl. 7, figs 7–9.
- 1988 *Terebratulina gracilis* (Schlotheim); Johansen, fig. 2; pl. 1, fig. 5a, b.

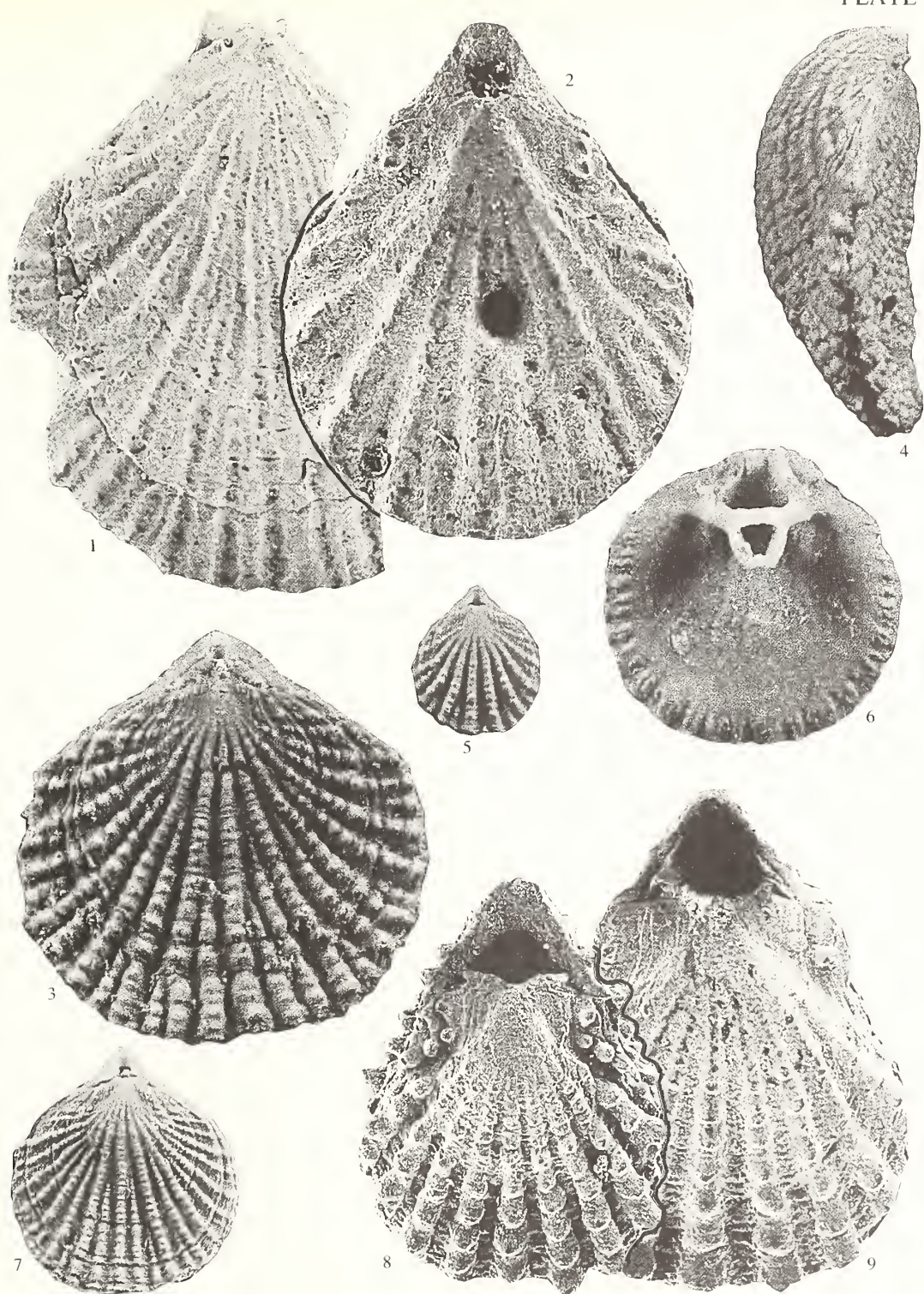
Material. Fifty complete shells, 320 dorsal and 170 ventral valves, and more than 1200 fragments. Largest specimen from Sidestrand 2 (lower Lower Maastrichtian) representing ventral valve medium sized adult: length, 3.4 mm; width, 3.2 mm; dorsal valve length, 3.4 mm; width of foramen, 0.3 mm; 30 ribs. Material also contains fragments from larger specimens, but no usable measurements have been obtained from these. Catalogue numbers MGUH 16858, 16859; SPGIH 3535–3538.

Description. Shells large, thick. Outline changes from elongated oval to subcircular during growth. Juvenile shells are biconvex, ventral valve of highest convexity; adults plano-convex. Very early growth stages possess 8–10 straight finely knobbed strong radial ribs forming characteristic fanlike pattern. At shell length of approximately 1.5 mm lateral deflection of ribs begins; at this stage new ribs form by intercalation. Large specimens may possess 50–60 ribs. Hinge line very short, oblique; auricles small. Beak short, erect to somewhat incurved; foramen oval, submesothyridid to permesothyridid and small throughout ontogeny. Hinge strong; brachidium consists of thin crura and closed brachial ring. Probably plectolophe.

EXPLANATION OF PLATE 4

Figs 1–7. *Terebratulina gracilis* (Schlotheim, 1813). 1, MGUH 16858, upper Lower Maastrichtian, Little Marl Point 7, Norfolk; broken adult dorsal valve in exterior view showing lateral bend of ribs, $\times 15$. 2, MGUH 16859, upper Lower Maastrichtian, Little Marl Point 3, Norfolk; large juvenile in dorsal view, $\times 30$. 3 and 4, SPGIH 3535, lower Lower Maastrichtian, G 148–150, Kronsnoor; 3, adult specimen in dorsal view, $\times 10$; 4, lateral view showing reclining profile, $\times 10$. 5, SPGIH 3536, lower Lower Maastrichtian, G 148–150, Kronsnoor; small juvenile specimen in dorsal view, $\times 5$. 6, SPGIH 3537, lower Lower Maastrichtian, G 148–150, Kronsnoor; interior of adult dorsal valve showing ring-formed brachidium, $\times 8$. 7, SPGIH 3538, lower Lower Maastrichtian, G 148–150, Kronsnoor; large juvenile in dorsal view, $\times 8$.

Figs 8 and 9. *Terebratulina faujasii* (Roemer, 1841). 8, MGUH 16860, upper Lower Maastrichtian, Trimingham 1, Norfolk; adult specimen in dorsal view, $\times 22$. 9, MGUH 16861, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 2A, Norfolk; adult specimen in dorsal view, $\times 30$.



Remarks. The species is consistent with descriptions of *Terebratulina gracilis* (Schlotheim) by, for example, Steinich (1965) and Johansen (1987a). *Terebratulina gracilis* differs from other species of *Terebratulina* in the plano-convex shell, short incurved beak, very small foramen and the high number of deflected ribs. Later forms of *T. gracilis* (e.g. from the Upper Maastrichtian of Denmark) possess almost concavo-convex shells and highly incurved beaks; these two features represent modifications for a free living mode of life on soft chalk substrates and presumably had not yet reached optimum development in the Upper Campanian–Lower Maastrichtian.

Gisilina gisii (Roemer) differs from juvenile *T. gracilis* in having straight, faintly nodate or almost smooth ribs.

Throughout the literature *T. gracilis* has been confused with *Terebratulina rigida* (J. Sowerby). Schloenbach (1866) described and compared *T. gracilis* and *T. rigida* and from both his descriptions and illustrations it is clear that *T. rigida* is smaller and possesses a less incurved beak and much less reflexed ribs than *T. gracilis*. *T. rigida* or a close relative is present in the Norfolk material. It is described below as *T. cf. rigida* and is slightly biconvex, possesses finely knobbed ribs which are only very slightly reflexed in large forms and possesses a distinct hinge line. It has, however, not in all cases been possible to separate the two species, but the material is dominated by *T. gracilis*.

Occurrence. Cley?, Keswick, Catton 3A and 4, Stoke Holy Cross 1, Catton 5 and 6, Caistor 3 and 1?, Whitlingham, Overstrand Hotel Lower Mass, Bramerton?, Overstrand Hotel Upper Mass 1A, 1, 2?, 2A, 3? and 4, Sidestrand 1A?, 2, 3?, 3A and 4?, Little Marl Point 1B, 1, 1A, 2, 2A? and 3, Trimingham 1, Little Marl Point 4, 5, 6 and 7, and Trimingham 2 and 3. *Terebratulina gracilis* is in addition known from the Upper Campanian and Maastrichtian of northern Germany, and the Maastrichtian of the Netherlands, Denmark, southern Sweden and eastern Poland.

Terebratulina longicollis Steinich, 1965

Plate 5, figs 4 and 5

- 1965 *Terebratulina longicollis* Steinich, p. 66, figs 62–75, pl. 8, fig. 2a–d.
- 1972 *Terebratulina longicollis* Steinich; Surlyk, p. 18, figs 5, 12–15, 17, 18.
- 1979 *Terebratulina longicollis* Steinich; Bitner and Pisera, p. 75, pl. 3, figs 9–11.
- 1982 *Terebratulina longicollis* Steinich; Surlyk, fig. 1, pl. 1, fig. e.
- 1984 *Terebratulina longicollis* Steinich; Surlyk and Johansen, fig. 1.
- 1987a *Terebratulina longicollis* Steinich; Johansen, p. 16, figs 15A–F; pl. 7, figs 4–6.
- 1988 *Terebratulina longicollis* Steinich; Johansen, fig. 2, pl. 2, fig. 11.

Material. Seven complete specimens, four dorsal and six ventral valves. Largest specimen is from Little Marl Point 3: length, 2.8 mm; width, 1.7 mm; length of dorsal valve, 2.2 mm; thickness, 1.0 mm; 9 ribs. Catalogue numbers MGUH 16865; SPGIH 3539.

Description. Outline elongate subpentagonal. Auricles small, but clearly defined. Biconvex, ventral valve the more convex. Commissure is straight. At 0.5 mm width there are 6–8 radial ribs; larger specimens normally have 8–10 ribs. Width and height of ribs increases during growth; new ribs occasionally form in the auricular

EXPLANATION OF PLATE 5

- Figs 1–3. *Terebratulina cf. rigida* (J. de C. Sowerby, 1821), lower Upper Campanian, Catton 1, Norfolk. 1, MGUH 16862, exterior of medium-sized dorsal valve, $\times 20$. 2, MGUH 16863, medium-sized specimen in dorsal view, $\times 30$. 3, MGUH 16864, interior of adult ventral valve showing recrystallized spicular skeleton of a plectolophe, brachidium itself is broken off, $\times 25$.
- Figs 4 and 5. *Terebratulina longicollis* Steinich, 1965. 4, SPGIH 3539, upper Upper Campanian, G 142, Kronsnoor; adult specimen in dorsal view, $\times 25$. 5, MGUH 16865, upper Lower Maastrichtian, Little Marl Point 3, Norfolk; interior of adult ventral valve showing large foramen, $\times 30$.



regions external to first formed ribs; no intercalated ribs. Ribs straight; sculpture comprises small crescentic nodes. Rib sculpture strongest on the ventral valve. Rib width is 1.5 times the width of interspaces; 1–2 growth lines. Beak suberect, short, the cardinal area very narrow, sharply delimited. Foramen initially hypothyriddid, later mesothyridid. Deltidial plates converge anteriorly during growth resulting in subcircular foramen. Pedicle collar well developed. Inner socket ridges high, thin, long; outer socket ridges low. Hinge teeth relatively strong, pointed. Brachidium begins to form at 0.6 mm width. Fully developed terebratulid brachidium attained at width about 1.5 mm (see Steinich 1965, fig. 71).

T. longicollis possesses a well-developed spicular skeleton in mantle, anterior body wall, and lophophore arms. Plectolophe at maturity.

Inner shell surface has smooth topography matching that of exterior. Shell relatively thick.

Remarks. *T. longicollis* can be distinguished from *T. chrysalis* (Schlothheim) by its undivided ribs. Juvenile *T. chrysalis*, in which intercalation of new ribs has not appeared, are always relatively wider, and the ribs lack the crescentic sculpture of *T. longicollis*. The ribs of *T. longicollis* are furthermore much more closely-spaced. *T. longicollis* resembles *T. faujasii* (Roemer) in that both have undivided ribs and similar rib sculpture, but they can always be distinguished by the very elongate outline of *T. longicollis*.

Occurrence. Whitlingham, Bramerton, Overstrand Hotel Upper Mass 1A and 2A, Little Marl Point 2 and 3, and Trimmingham 3. The species is in addition recorded from the Upper Campanian and Maastrichtian of northern Germany and eastern Poland, and from the Maastrichtian and possibly also Lower Danian of Denmark.

Terebratulina cf. *rigida* (J. Sowerby, 1829)

Plate 5, figs 1–3

cf. 1829 *Terebratula rigida* J. Sowerby, p. 69, pl. 536, fig. 2.

cf. 1866 *Terebratulina rigida* (J. Sowerby); Schloenbach, p. 287, pl. 38, figs 10–17.

Material. Eleven complete shells, twelve dorsal, thirty-two ventral valves, and a large number of fragments. Largest complete specimen is juvenile from Catton 1: length, 3.8 mm; width, 3.1 mm; length of dorsal valve, 2.8 mm; thickness, 1.3 mm; width at hinge line, 1.0 mm; width of foramen, 0.5 mm; 21 ribs. Catalogue numbers MGUH 16862–16864.

Description. Shell relatively large, biconvex, outline subtriangular, rather thick and punctuate. Auricles small but distinct; hinge line straight. At shell width 2.0 mm, shell bears 10 ribs, at 2.5 mm, 18–20 ribs and at 3.0 mm 23–25 ribs. New ribs arise by intercalation; ribs straight to slightly reflexed in larger specimens. Rib sculpture consists of closely-spaced transverse half rings, most prominent on ventral valve. Beak erect, blunt to slightly incurved; foramen rather large, broad, triangular to elongate oval. Deltidial plates high, triangular, converging; internal morphology otherwise poorly known. Plate 5, fig. 3 shows a recrystallized spicular skeleton from a plectolophous lophophore.

Remarks. *T. gracilis* and *T. rigida* have been confused since their descriptions in 1813 and 1821 respectively (Schloenbach 1866; J. Sowerby 1829). Steinich (1965) and Johansen (1987a) both mention this problem. *T. rigida* is in general smaller, possesses a larger foramen, a less incurved beak and ribs much less reflexed than in *T. gracilis*. The Norfolk specimens correspond to *T. rigida*, but as the material does not permit detailed observations of internal morphology, we refer to the material as *T. cf. rigida*.

T. chrysalis differs from *T. cf. rigida* in possessing a more elongated outline, and more ribs, which retain their width during growth.

Occurrence. Catton 1, 3, 4 and 6, Sidestrand 1A? and 2?, Little Marl Point 1B?, and Trimmingham 2.

Terebratulina subtilis Steinich, 1965

Plate 6, figs 1 and 2

- 1965 *Terebratulina subtilis* Steinich, p. 93, figs 115–129; pl. 9, fig. 2a–d.
 1970b *Terebratulina subtilis* Steinich; Surlyk, p. 13, fig. 3.
 1972 *Terebratulina subtilis* Steinich; Surlyk, p. 18, fig. 2.
 1982 *Terebratulina subtilis* Steinich; Surlyk, fig. 1.
 1988 *Terebratulina subtilis* Steinich; Johansen, fig. 2.

Material. Eleven complete shells, twenty-six dorsal, twenty-five ventral valves, and thirty-five fragments. The largest specimen is from Little Marl Point 6: length, 2.5 mm; width, 2.0 mm; thickness, 0.8 mm; length of dorsal valve, 2.1 mm; 48 ribs. Catalogue numbers MGUH 16866, 16867.

Description. Shell thin with smooth interior. Outline very elongate subpentagonal to subtriangular in juvenile stages, changing into more pointed oval with growth. Biconvex to almost plano-convex; dorsal valve normally convex umbonally, otherwise flat. Auricles poorly-defined; commissure straight. Ornament consists of numerous delicate radial ribs. At a width of c. 0.5 mm, 3–10 relatively wide ribs appear. New ribs arise by intercalation and are always narrower than earlier formed ribs. Specimens 2 mm or more wide have 40–50 ribs of very low amplitude bearing a characteristic sculpture of small granules often somewhat coarser on ventral than on dorsal valve, where they may be very difficult to detect. Growth lines indistinct or absent. Beak short, suberect, cardinal area narrow, but well-defined. Foramen limited by two narrow triangular deltidial plates; develops from hypothyriddid to submesothyridid during growth. Pedicle collar wide, well-developed. Hinge rather weakly-developed; inner socket ridges thin. Brachidium develops at a width 0.4 mm; normal, rather delicate terebratulined brachidium present at width c. 1.3 mm.

Spicular skeleton well-developed, normally strongly recrystallized. Plectolophe. Mantle spicules not found.

Remarks. *Terebratulina subtilis* shows great resemblance to *Rugia tenuicostata* Steinich, and the juveniles of the two species are particularly difficult to separate. *T. subtilis*, however, always has a larger number of ribs, and a less pointed beak. The most important difference is in the rib morphology where *R. tenuicostata* has rather high, relatively widely-spaced serrate ribs, while *T. subtilis* has flat densely-spaced ribs with only small rather rounded tubercles.

Occurrence. Keswick?, Catton 1, 3 and 5, Overstrand Hotel Lower Mass, Overstrand Hotel Upper Mass 1A, 1 and 2, Sidestrand 2 and 3A, Little Marl Point 2A, Trimingham 1, Little Marl Point 6 and 7, and Trimingham 3. In addition, the species is known from the Lower Maastrichtian of northwest Germany, East Germany and Denmark.

Genus GISILINA Steinich, 1963

Type species. *Terebratula gisii* Roemer, 1841, p. 40, fig. 23.

Gisilina gisii (Roemer, 1841)

Plate 6, figs 3–5

- 1841 *Terebratula gisii* Roemer, p. 40, fig. 23.
 1963b *Gisilina gisii* (Roemer); Steinich, p. 732, figs 1–8.
 1965 *Gisilina gisii* (Roemer); Steinich, p. 100, figs 130–148; pl. 14, figs 2 and 3a–d; pl. 15, figs 1–7.
 1972 *Gisilina gisii* (Roemer); Surlyk, p. 18, figs 2, 12, 20–22.
 1982 *Gisilina gisii* (Roemer); Surlyk, fig. 1, pl. 2, fig. d.
 1988 *Gisilina gisii* (Roemer); Johansen, fig. 2.

Material. Three complete shells, eleven dorsal, six ventral valves, and one fragment. Largest specimen is a dorsal valve from Caistor 1: length of dorsal valve, 3.1 mm; width, 3.2 mm; 12 ribs. Catalogue numbers MGUH 16868; SPGIH 3540.

Description. Outline rounded subtriangular; auricles small, indistinct. Shell rather thick, strongly biconvex, ventral valve having highest convexity. Shell surface with 7–12 straight, coarse, broad, smooth or faintly nodate ribs. New ribs arise by intercalation. Beak changes from acute and suberect to slightly incurved or erect during ontogeny. Foramen large, initially hypothyriddid, thereafter submesothyridid and in some cases

mesothyridid in large forms, and thus partly absorbed in ventral valve. Inner socket ridges short and teeth strong. Little can be said of the brachidium in present material: crura very short. Probably a plectolophe.

Remarks. Large specimens of *G. gisii* are easily distinguished from *G. jasmundi* Steinich because they are more strongly biconvex, have smooth to faintly nodate ribs, and a mesothyridid foramen. Small specimens are very difficult to distinguish from juvenile *Terebratulina chrysalis* (Schlotheim) and *G. jasmundi*. *G. gisii* has fewer ribs than *T. chrysalis* and is more biconvex. *G. jasmundi* is less biconvex than *G. gisii* and has distinctly coarser sculpted ribs. Ribs are single in *G. jasmundi*.

Occurrence. Caistor 1, Overstrand Hotel Lower Mass, Overstrand Hotel Upper Mass 1A, 2 and 3, Little Marl Point 7, and Trimmingham 2. The species is also recorded from the Upper Campanian and Maastrichtian of northwest Germany, and the Maastrichtian of East Germany, southern Sweden and Denmark.

Gisilina jasmundi Steinich, 1965

Plate 6, fig. 6

- 1965 *Gisilina jasmundi* Steinich, p. 110, figs 149–161; pl. 16, figs 1a–d and 2.
- 1972 *Gisilina jasmundi* Steinich; Surlyk, p. 18, figs 2, 5, 13, 15a, 16, 17.
- 1982 *Gisilina jasmundi* Steinich; Surlyk, fig. 1, pl. 2, figs a–c.
- 1984 *Gisilina jasmundi* Steinich; Surlyk and Johansen, fig. 1.
- 1987a *Gisilina jasmundi* Steinich; Johansen, p. 21, pl. 8, fig. 3.
- 1988 *Gisilina jasmundi* Steinich; Johansen, fig. 2.

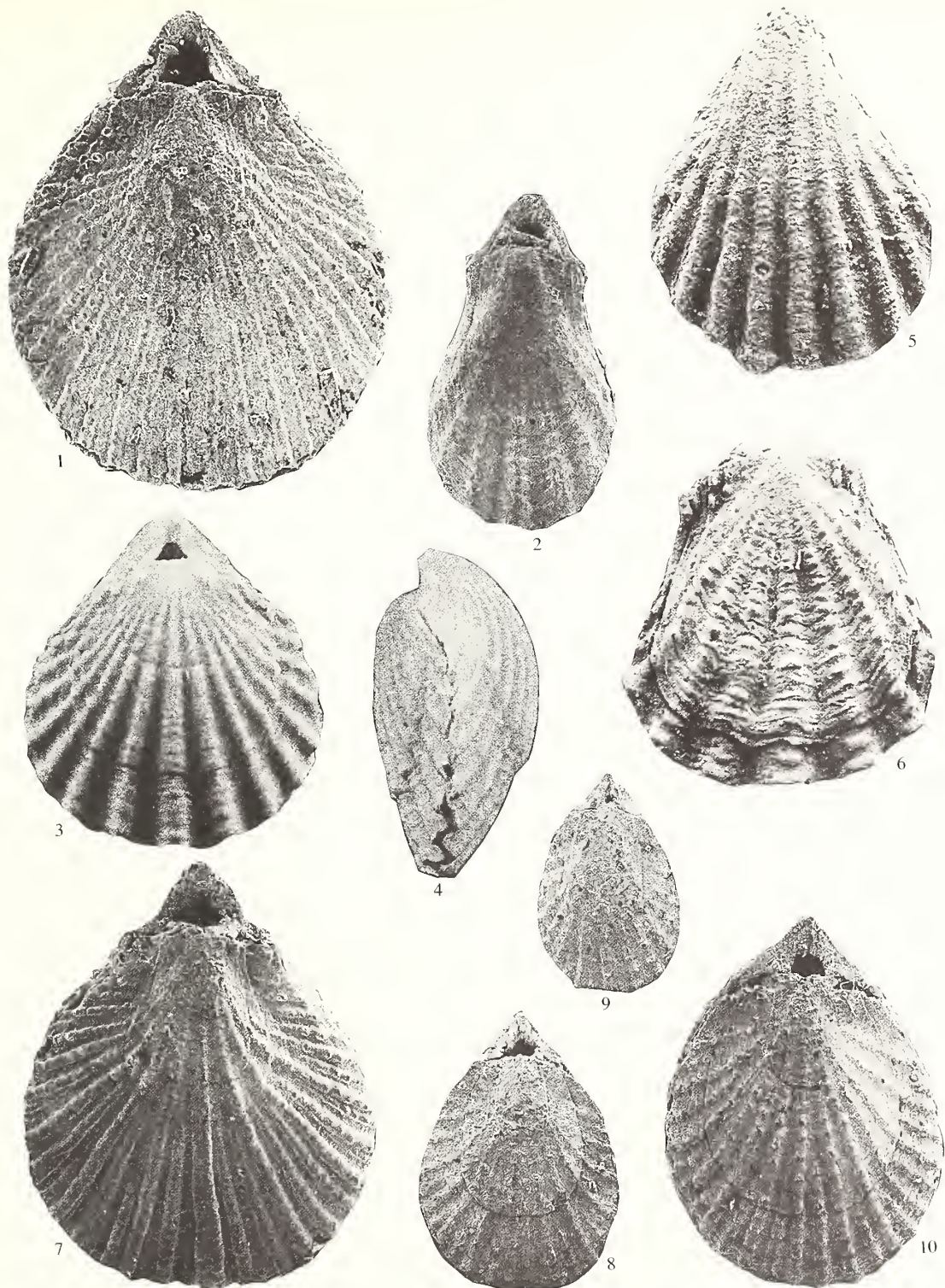
Material. At least one complete shell, twelve dorsal, two ventral valves, and four fragments. Largest specimen represented by ventral valve from Sidestrand 1: length, 3.8 mm; width, 3.0 mm; length of dorsal valve, 3.0 mm; width of hinge line, 2.4 mm; 13 ribs. Catalogue number MGUH 16869.

Description. Norfolk specimens have subtriangular to subpentagonal outline and small but distinct auricles. Beak suberect, foramen large, submesothyridid. Hinge line short, straight. Characteristic for this species are 12–18 straight, radial, and coarsely nodate single ribs, and a relatively flat shell. Rib sculpture varies between coarse knobs on top of ribs and prominent transverse half rings arranged across the ribs. Inner socket ridges high, teeth short. Crura short, other details of brachidium not seen. Probably plectolophe.

Remarks. *G. jasmundi* is thoroughly described by Steinich (1965). Large specimens of *G. jasmundi* recall *Terebratulina faujasii* (Roemer), but differ in the larger number of ribs, flatter shell, and finer

EXPLANATION OF PLATE 6

- Figs 1 and 2. *Terebratulina subtilis* Steinich, 1965. 1, MGUH 16866, lower Upper Campanian, Keswick, Norfolk; dorsal view of adult specimen, $\times 30$. 2, MGUH 16867, lowermost Maastrichtian, Overstrand Hotel Upper Mass 1A, Norfolk; dorsal view of juvenile specimen, $\times 30$.
- Figs 3–5. *Gisilina gisii* (Roemer, 1841). 3 and 4, SPGIH 3540, lower Upper Campanian, G 140, Lägerdorf; 3, adult specimen in dorsal view, $\times 18$. 4, lateral view showing strongly biconvex shell, $\times 18$. 5, MGUH 16868, upper Lower Maastrichtian, Trimmingham 2, Norfolk; medium-sized adult ventral valve in exterior view, $\times 25$.
- Fig. 6. *Gisilina jasmundi* Steinich, 1965. MGUH 16869, uppermost Campanian, Overstrand Hotel Lower Mass, Norfolk; medium-sized adult ventral valve in exterior view, $\times 25$.
- Fig. 7. *Rugia tenuicostata* Steinich, 1963. MGUH 16870, lower Upper Campanian, Keswick, Norfolk; adult specimen in dorsal view, $\times 25$.
- Figs 8–10. *Rugia acutirostris* Steinich, 1965, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 2A, Norfolk. 8, MGUH 16871, juvenile in dorsal view, $\times 27$. 9, MGUH 18226, Norfolk; small juvenile in dorsal view, $\times 20$. 10, MGUH 18227, adult specimen in dorsal view, $\times 25$.



sculptured rib surface. Small specimens of *G. jasmundi* with more faintly sculptured ribs are extremely difficult to distinguish from juveniles of *G. gisii* (Roemer) and *T. chrysalis* (Schlotheim). Juvenile *G. jasmundi* possess coarse sculptured, single ribs; *T. chrysalis* is elongate and has intercalated ribs.

Occurrence. Overstrand Hotel Lower Mass, Overstrand Hotel Upper Mass 1A and 3?, and Sidestrand 1. In addition, the species is recorded from the Maastrichtian of northwest Germany, East Germany and Denmark.

Genus RUGIA Steinich, 1963

Type species. *Rugia tenuicostata* Steinich, 1963b, p. 735, fig. 3.

Rugia tenuicostata Steinich, 1963

Plate 6, fig. 7

- 1963b *Rugia tenuicostata* Steinich, p. 738, figs 6, 7, 8a-d.
- 1965 *Rugia tenuicostata* Steinich; Steinich, p. 116, figs 162-174; pl. 11, 3a-d and 4.
- 1970 *Rugia tenuicostata* Steinich; Surlyk, figs 2 and 3.
- 1972 *Rugia tenuicostata* Steinich; Surlyk, p. 8, figs 2, 5, 12, 16.
- 1979 *Rugia tenuicostata* Steinich; Bitner and Pisera, p. 77, pl. 4, figs 3-6; pl. 5, fig. 3.
- 1982 *Rugia tenuicostata* Steinich; Surlyk, fig. 1, pl. 1, figs f-h.
- 1984 *Rugia tenuicostata* Steinich; Surlyk and Johansen, fig. 1.
- 1987a *Rugia tenuicostata* Steinich; Johansen, p. 22, figs 18F, G, pl. 7, fig. 2.
- 1987b *Rugia tenuicostata* Steinich; Johansen, p. 159, figs 3, 14A-F; pl. 6, figs 1-5.
- 1988 *Rugia tenuicostata* Steinich; Johansen, fig. 2, pl. 2, fig. 1.

Material. Seventeen complete shells, eighty-one dorsal, sixty-nine ventral valves, and one hundred fragments. Largest specimen from Keswick: length, 2.48 mm; width, 2.04 mm; length of dorsal valve, 2.12 mm; thickness, 0.96 mm; 41 ribs. Catalogue number MGUH 16870.

Description. Outline very elongate subtriangular in early growth stages, changing through ontogeny to more pointed oval. Shell is biconvex; dorsal valve always less convex than ventral valve. Inner shell smooth. Some juvenile specimens may have completely flat dorsal valve. Auricles indistinct. Commissure straight. Shell ornamentation of straight radial ribs with serrate sculpture. Initial ribs are formed at width 0.4 mm, number increases by intercalation from about 6-7 to 28-30. In rare cases large forms have 40 ribs, but last 10 ribs are very narrow low intercalatories close to shell margin. Ribs are of uniform height and width through ontogeny. Rib density varies considerably, decreasing markedly during ontogeny. Rib sculpture highly characteristic, comprising small triangular tubercles aligned on top of ribs, giving saw-tooth appearance. New intercalated ribs often form an acute angle to adjacent older ribs but change to more parallel alignment during growth. Growth lines uncommon. beak short, suberect, pointed in juvenile stages; more rounded in adult forms. Cardinal area narrow, well-defined. Foramen delineated by two narrow deltidial plates, which grow in ventro-median direction in the earliest stages; at shell width of 0.6 mm they grow outwards in ventro-lateral direction; at width of 0.7 mm growth direction changes to median. Pedicle collar increases relative length in growth to half length of beak. Foramen triangular, hypothyridid. Hinge close to that of *Terebratulina*. Brachidium consists of long, thin crura, converging strongly anteriorly. Crural processes short, spoon-shaped, not fused during growth. Descending branches thin, fusing under acute angle. Mantle and arms heavily spiculate; lophophore plectolophe.

Remarks. *R. tenuicostata* can be distinguished from *R. acutirostris* Steinich by the less acute beak, lower rib density, and characteristic rib sculpture. Juveniles are difficult to separate from *Terebratulina subtilis* Steinich, other than by the rib characters; *T. subtilis* has numerous weakly sculptured very low ribs.

Occurrence. Cley, Keswick, Catton 1?, 3, 3A and 4, Stoke Holy Cross 1, Catton 5 and 6, Caistor 3 and 1, Whitlingham, Overstrand Hotel Upper Mass 1A, Little Marl Point 1?, 1A and 5?. Also known from the Upper Campanian to Maastrichtian of northwest and East Germany, Denmark and Poland.

Rugia acutirostris Steinich, 1965

Plate 6, figs 8–10

- 1965 *Rugia acutirostris* Steinich, p. 122, figs 175–178; pl. 14, 1a–d.
 1970 *Rugia acutirostris* Steinich; Surlyk, figs 2 and 3.
 1972 *Rugia acutirostris* Steinich; Surlyk, p. 18, figs 2, 5, 14, 18.
 1979 *Rugia acutirostris* Steinich; Bitner and Pisera, p. 77, pl. 3, figs 1–3.
 1982 *Rugia acutirostris* Steinich; Surlyk, fig. 1, pl. 1, figs *i* and *j*.
 1984 *Rugia acutirostris* Steinich; Surlyk and Johansen, fig. 1.
 1987a *Rugia acutirostris* Steinich; Johansen, p. 22, pl. 7, fig. 1A, B.
 1987b *Rugia acutirostris* Steinich; Johansen, p. 163, figs 3, 15A–F; pl. 5, fig. 4.
 1988 *Rugia acutirostris* Steinich; Johansen, fig. 3.

Material. Thirty-eight complete shells, sixty dorsal, thirty-seven ventral valves, and sixty fragments. Largest specimen is from Overstrand Hotel Upper Mass 1A: length, 2.0 mm; length of dorsal valve, 1.7 mm; width, 1.5 mm; thickness, 0.8 mm; 26 ribs. Catalogue numbers MGUH 16871, 18226, 18227.

Description. Outline changes from elongate subpentagonal to pointed oval during ontogeny. Auricles small, blunt. Shell biconvex, the valves of equal convexity. 6–8 radial ribs are present at shell width of 0.2–0.3 mm. Ribs increase in number by intercalation to about 40. Rib width constant during growth. Rib sculpture consists of small, scale-like tubercles; in some specimens ribs are smooth. Lateral ribs curve slightly outwards. Beak very acute, suberect. Cardinal area wide, clearly delineated, triangular, slightly concave. Foramen very small, elongate triangular, hypothyridid, limited by two narrow slightly elevated deltidial plates, often granular. Pedicle collar very long. Hinge and brachidium development as in *R. tenuicostata*. Inner surface of shell is smooth. The mantle and arms heavily spiculate. Plectolophe.

Remarks. *R. acutirostris* is characterized by its pointed oval outline, its very acute beak, and small foramen.

Occurrence. Overstrand Hotel Lower Mass, Bramerton, Overstrand Hotel Upper Mass 1A, 1, 2A, 3 and 4, Sidestrand 1, 1A, 3A and 4, and Little Marl point 5 and 7. Also known from both the Lower and Upper Maastrichtian of northwest and East Germany, Denmark and Poland.

Rugia tegulata Surlyk, 1970

Plate 7, figs 1 and 2

- 1970a *Rugia tegulata* Surlyk, p. 152, pl. 1, figs *a–e*, fig. 4a–d.
 1972 *Rugia tegulata* Surlyk; Surlyk, p. 18, fig. 5.
 1984 *Rugia tegulata* Surlyk; Surlyk, fig. 2.
 1988 *Rugia tegulata* Surlyk; Johansen, fig. 2.

Material. Five dorsal, three ventral valves, and four fragments. Largest specimen a dorsal valve: length, 1.6 mm; width, 1.9 mm; 21 ribs. Catalogue numbers MGUH 18228–9.

Description. Outline subtriangular to pointed oval; length to width ratio decreases rapidly during growth. Auricles blunt; shell slightly biconvex, dorsal valve being a little less convex than ventral valve. Ornament very characteristic; radial ribs with imbricate, plate-like scales. Rib number increases rapidly by intercalation from about 5 at width 0.5 mm to about 20 in largest specimens. Beak suberect; cardinal area small. Foramen is triangular, hypothyridid, limited by two deltidial plates which often take the form of irregular ridges with constriction at middle of each plate. Inner socket ridges short, strong. Crurae long, thin; full brachidium is not preserved. Shell is rather thick; gentle undulations on inner surface correspond to the ribs on outer.

Remarks. Although limited the material falls well within the range of the type material from the lower Upper Maastrichtian of Denmark. The characteristic rib sculpture distinguishes it from other Chalk brachiopods.

Occurrence. All specimens are from Little Marl Point 1A. The species has previously been described only from the lower Upper Maastrichtian of Denmark.

Rugia spinosa Surlyk, 1970

- 1970a *Rugia spinosa* Surlyk, p. 157, fig. 3d-f; pl. 2, figs a-d; table 1.
 1972 *Rugia spinosa* Surlyk; Surlyk, p. 18, figs 2, 5.
 1982 *Rugia spinosa* Surlyk; Surlyk, p. 262, fig. 1.
 1984 *Rugia spinosa* Surlyk; Surlyk, p. 219, figs 2 and 3.
 1987b *Rugia spinosa* Surlyk; Johansen, p. 157, figs 3, 11A-F, 12A, B, 13.
 1988 *Rugia spinosa* Surlyk; Johansen, fig. 2.

Material. One fragmentary valve and two fragments.

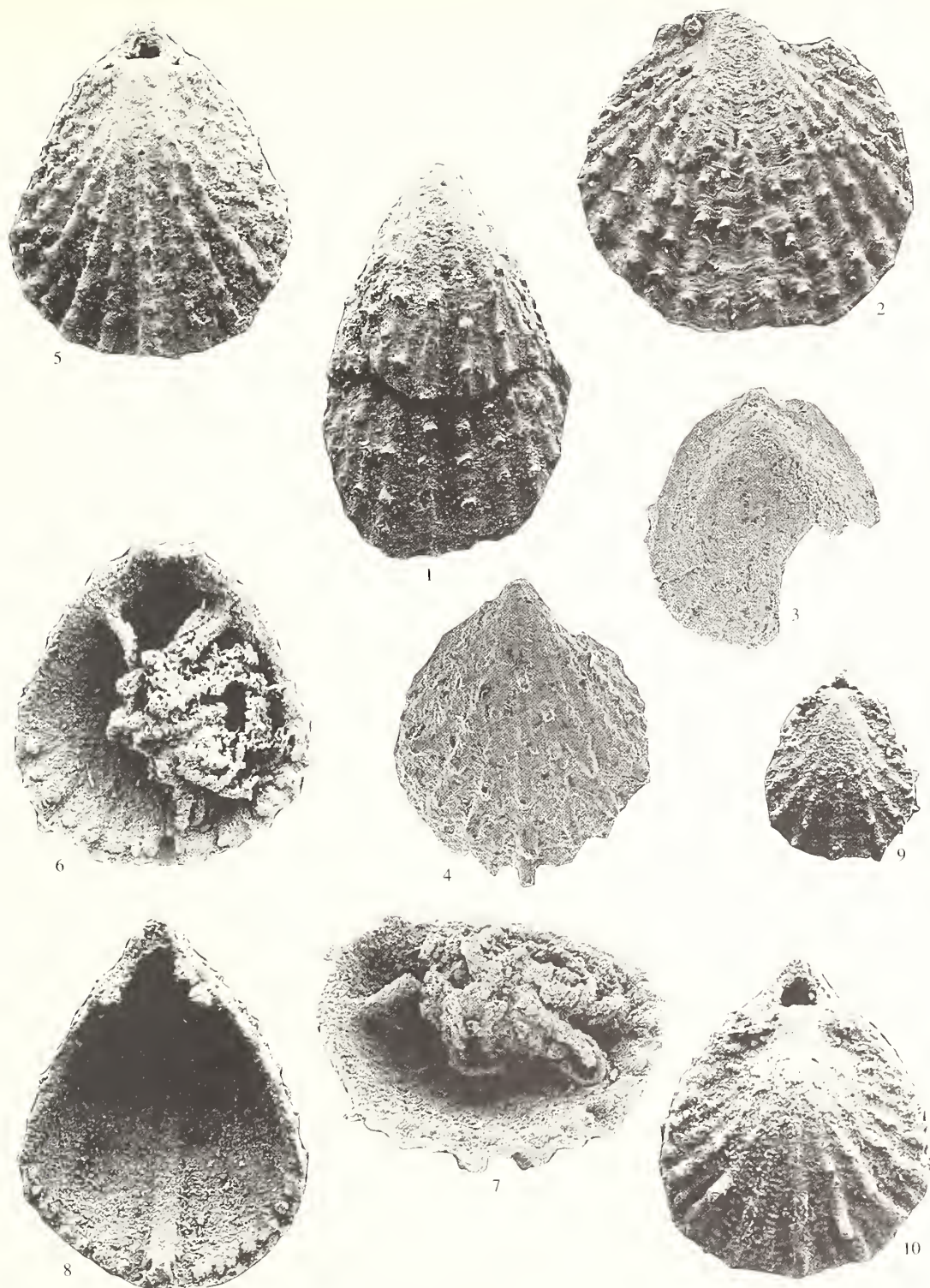
Description. Shell small and thin, outline oval to pointed oval. Auricles are blunt. Shell strongly biconvex, anterior commissure straight. Shell sculpture comprises long, pointed spines of variable form and size in many cases extending from irregular, poorly-developed radial ribs. They tend to be at right angles to the shell surface on the posterior part of the shell, while larger and directed forwards in the anterior part of shell. Spines may be arranged in rows, on a more-or-less distinctly developed rib. Ribs few in number, irregularly distributed, often best seen on inside of shell as strong, well-defined smooth ribs. Beak very short, pointed and suberect. Cardinal area and deltidial plates narrow. Foramen very small, submesothyrilid. Inner socket ridges short with anterior lateral bend, close together. Teeth short, pointed. Crura thin, cylindrical, originating from position anterior to inner socket ridges. Inner surface of the shell smooth apart from a few irregularly distributed ribs.

Remarks. *R. spinosa* is characterized by its rib sculpture; it differs from *R. spinicostata* Johansen and Surlyk in having only a few irregularly distributed ribs. Bitner and Pisera (1979) emended the original diagnosis of *R. spinosa* to include forms with regularly distributed ribs, but study of abundant stratigraphically well-dated material of this form from eastern England, northwest Germany and Denmark shows that lower Lower Maastrichtian forms are *R. spinosa*, while Upper Campanian forms belong to *R. spinicostata*, described below (Surlyk 1982; Johansen 1987b). Bitner and Pisera (1979) assigned the Mielnik chalk section, eastern Poland to the Lower Maastrichtian because of the presence of *R. spinosa* in the lower part of the section, but the Polish material clearly belongs to *R. spinicostata*. The lower part of the Mielnik section is thus most probably of Late Campanian age.

Occurrence. Overstrand Hotel Upper Mass 1A and 2A. Also known from the lower Lower Maastrichtian of Denmark and northwest and East Germany.

EXPLANATION OF PLATE 7

- Figs 1 and 2. *Rugia tegulata* Surlyk, 1970. 1, MGUH 18228, lower Lower Maastrichtian, Little Marl Point 1A, Norfolk; exterior of broken ventral valve, $\times 30$. 2, MGUH 18229, lower Lower Maastrichtian, Little Marl Point 1A, Norfolk; exterior of dorsal valve, $\times 20$.
 Figs 3-10. *Rugia spinicostata* Johansen and Surlyk in Johansen, 1987b. 3, MGUH 18230, upper Upper Campanian, Catton 3A, Norfolk; interior of broken adult dorsal valve, $\times 25$. 4, MGUH 18231, upper Upper Campanian, Cley, Norfolk; ventral valve in exterior view, $\times 25$. 5, SPGIH 3541, upper Lower Campanian, G 81, Lägerdorf; adult specimen in dorsal view, $\times 30$. 6 and 7, SPGIH 3542A, lower Upper Campanian, G 103, Lägerdorf; 6, interior of adult dorsal valve showing almost complete spoon-shaped brachidium and recrystallized plectolophous lophophore, $\times 30$; 7, oblique lateral view showing long recrystallized spicular skeleton of lophophore filaments, $\times 30$. 8, SPGIH 3542B, interior of ventral valve corresponding to dorsal valve shown on figs 6 and 7, $\times 30$. 9, SPGIH 3543, upper Lower Campanian, G 78, Lägerdorf; juvenile in dorsal view, $\times 20$. 10, SPGIH 3544, lower Upper Campanian, G 103, Lägerdorf; dorsal view, $\times 30$.



Rugia spinicostata Johansen and Surlyk, 1987 in Johansen, 1987b

Plate 7, figs 3–10

- 1979 *Rugia spinosa* Surlyk; Bitner and Pisera, p. 78, pl. 3, figs 4–8.
 1982 *Rugia spinosa* s.l. Surlyk; Surlyk, p. 262, fig. 1.
 1984 *Rugia spinosa* s.l. Surlyk; Surlyk, p. 219, fig. 2.
 1987b *Rugia spinicostata* Johansen and Surlyk; Johansen, p. 152, figs 3 and 11A–F; pl. 5, figs 1–3.
 1988 *Rugia spinicostata* Johansen and Surlyk; Johansen, fig. 2, pl. 2, fig. 2.

Material. Five dorsal, six ventral valves, and three fragments. Largest Norfolk specimen a ventral valve from the upper Upper Campanian of Cley: length, 1.6 mm; width, 1.4 mm; length of dorsal valve, 1.3 mm; width of hinge line, 0.8 mm; foramen diameter, 0.2 mm; 22 ribs. Catalogue numbers MGUH 18230, 18231; SPGIH 3541, 3542A and B, 3543, 3544.

Description. Shell small, pointed oval to pointed subtriangular in outline. Strongly biconvex, anterior commissure straight. Auricles are blunt; stumpy. Surface sculpture of long, pointed spines extending from regularly distributed radial ribs, slightly reflexed in larger forms. Spines are cylindrical, pointed solid, variable in form and size. Spines arranged in rows on distinct ribs; in most cases spines are directed anteriorly. About 16 ribs present at shell width 1.0 mm; about 26 at 2.0 mm. Inside of the shell typically with very prominent, strong, smooth straight median rib and several straight and smooth ribs lateral to this. Beak short, suberect; cardinal area narrow. Deltidial plates narrow, triangular, foramen small, subtriangular, submesothyridid.

Structure of hinge and brachidium similar to *R. acutirostris* and *R. tenuicostata*. Inner socket ridges strong, short and close together, forming an antero-lateral bend. Cardinal process small, bulbous, protrudes well beyond posterior shell margin together with inner socket ridges. Teeth short, pointed, triangular. Crura long, thin, developing from anterior edge of inner socket ridges. Descending branches converge rapidly and fuse in strong bridge. Ascending branches short. Shell relatively thin. Plectolophe when adult.

Remarks. *R. spinicostata* differ from other *Rugia* species in possessing a surface sculpture of long, pointed spines extending from regularly distributed and distinct radial ribs; it was first recognized and described as a distinct form *Rugia spinosa* s.l. by Surlyk (1982).

The surface sculpture of *Rugia spinosa* Surlyk also consists of long, pointed spines, but in this species spines often extend from poorly-developed, irregular, radial ribs, which are fewer in number than in *R. spinicostata*. Ribs of *R. spinosa* often are recognized only from the inside of the shell as strong, smooth ridges (Surlyk 1970a).

R. spinosa is generally smaller than *R. spinicostata* and possesses a shorter and more pointed beak, and very close-lying, antero-laterally bent inner socket ridges (Johansen 1987b).

Occurrence. Cley, Keswick, and Catton 1, 3, 3A and 4. Also known from the Lower to the upper Upper Campanian of northwest Germany, and from possible Upper Campanian strata of eastern Poland (see discussion under *Rugia spinosa*).

Genus DRACIUS Steinich, 1967

Type species. *Dracius carnifex* Steinich, 1967, p. 1146, pl. 1, fig. 1.

Dracius carnifex Steinich, 1967

Plate 9, figs 5–8

- 1967 *Dracius carnifex* Steinich, p. 1145, figs 1–7; pl. 1, figs 1–4.
 1972 *Dracius carnifex* Steinich; Surlyk, figs 5, 16, 18.
 1982 *Dracius carnifex* Steinich; Surlyk, fig. 1, pl. 2, figs e and f.
 1988 *Dracius carnifex* Steinich; Johansen, fig. 2.

Material. One ventral valve and two fragments. Catalogue numbers MGUH 18241, 18242; SPGIH 3548, 3849.

Remarks. Limited material prevents detailed description, but characteristic ribbing of the ventral valve points to *D. carnifex*. Ribs at a shell length *c.* 0.5 mm are seen as 7–8 highly irregular rows of small spines. Ribs become stronger during growth and separation increases markedly. Ribs ornamented by small often spiny tubercles. Interspaces bear a dense cover of identical tubercles.

Occurrence. Whitlingham (?) and Overstrand Hotel Lower Mass. Also known from the Maastrichtian of East and northwest Germany and Denmark.

Family MEGATHYRIDIDAE Dall, 1870

Genus ARGYROTHECA Dall, 1900

Type species. *Terebratula cuneata* Risso, 1826, p. 388.

Argyrotheca brononii (Roemer, 1841)

Plate 8, figs 1–4, 7

- 1841 *Terebratula brononii* v. Hagenow; Roemer, p. 41, fig. 31.
- 1965 *Argyrotheca brononii* (Roemer); Steinich, p. 124, figs 179–196; pl. 17, figs 1*a–d* and 2*a–d*.
- 1972 *Argyrotheca brononii* (Roemer); Surlyk, p. 20, figs 5, 14–16; pl. 4*g*.
- 1979 *Argyrotheca brononii* (Roemer); Bitner and Pisera, p. 78, pl. 4, figs 1 and 2.
- 1982 *Argyrotheca brononii* (Roemer); Surlyk, fig. 1, pl. 3, figs *i* and *j*.
- 1984 *Argyrotheca brononii* (Roemer); Surlyk and Johansen, fig. 1.
- 1987*a* *Argyrotheca brononii* (Roemer); Johansen, p. 27.
- 1988 *Argyrotheca brononii* (Roemer); Johansen, fig. 2.

Material. Three complete shells, seventeen dorsal and twenty ventral valves, and twenty-seven fragments. Largest specimen is from Sidestrand 1: length, 2.52 mm; width, 3.32 mm; length of dorsal valve, 2.08 mm; thickness, 1.56 mm; eight ribs. Catalogue numbers MGUH 18232–3; SPGIH 3543, 3546.

Description. A very variable species. Outline semicircular to subpentagonal. Hinge margin often extended into small wings. Juveniles clearly biconvex, but plano-convex shape is rapidly attained. Rib number increases during growth from four to about eight. Ribs divided into two wide bundles, separated by shallow median sinus. Single ribs can develop in sinus at all stages of growth. Ribs rather flat, extending only slightly beyond shell margin; there are up to eight strong growth lines. Beak pointed; nearly straight to suberect. Cardinal area plane to slightly concave. Deltidial plates are narrow, foramen large, triangular. Pedicle collar well-developed with concave anterior margin. Inner socket ridges diverge strongly anteriorly. Cardinal process developed as low knob between posterior edges of inner socket ridges. Two concave circular separated hinge plates are situated anterior to the cardinal process. Brachidium is not preserved in present material. Dorsal median septum high, extended in ventral direction by attached distal ends of descending branches giving septum a characteristic split appearance. Ventral septum very thin, short. Inner surface of the shell is ornamented by a weak negative of external sculpture. Margin slightly elevated, finely tuberculated.

Remarks. The great variability of *A. brononii* results in morphological overlap with several other species. It can normally be separated from these on the basis of its rib number, split median septum, disjunct hinge plates and low median sinus.

Occurrence. Catton 5, Caistor 3 and 1, Overstrand Hotel Lower Mass, Overstrand Hotel Upper Mass 1A, 2A and 3, Sidestrand 1, 1A, 4 and 5, Little Marl Point 1, 5 and 6?, and Trimmingham 2. The species is also recorded from the Upper Campanian and Maastrichtian of England, the Netherlands, northwest and East Germany, eastern Poland and Denmark. In Denmark it also occurs in the Lower Danian.

Argyrotheca coniuncta Steinich, 1965

Plate 8, figs 5, 6, 8 and 9

- 1965 *Argyrotheca coniuncta* Steinich, p. 138, figs 200–206; pl. 18, fig. 2a–d.
 1972 *Argyrotheca coniuncta* Steinich; Surlyk, p. 20, figs 5–12.
 1979 *Argyrotheca coniuncta* Steinich; Bitner and Pisera, p. 79, pl. 5, figs 5–7.
 1982 *Argyrotheca coniuncta* Steinich; Surlyk, fig. 1, pl. 4, figs a–d.
 1984 *Argyrotheca coniuncta* Steinich; Surlyk and Johansen, fig. 1.
 1987a *Argyrotheca coniuncta* Steinich; Johansen, p. 28, pl. 12, fig. 5A, B.
 1988 *Argyrotheca coniuncta* Steinich; Johansen, fig. 2.

Material. One complete shell, nine dorsal, eight ventral valves, and six fragments. Largest specimen a dorsal valve from Overstrand Hotel Upper Mass 2: length of dorsal valve, 3.4 mm; width (which corresponds to the width of the hinge line), 7.0 mm; 12 ribs. Catalogue numbers MGUH 18234–18236; SPGIH 3547.

Description. Outline characteristically semicircular very often with wing-like extensions of the hinge line. Anterior commissure straight, shell flat biconvex, shell surface bears 6–12 low, straight ribs. Beak erect and characteristically strongly withdrawn. Foramen very large, hypothyridid, triangular; hinge strong; cardinal process small, anterior margins of inner socket ridges much longer than posterior. Hinge plates fused mid-dorsally into closed platform, sometimes seen as individual plates separated by median furrow. Dorsal median septum high, strong, not split. Shell surface with large punctae; rather thick.

Remarks. The specimens investigated correspond in many details to the originals of *A. coniuncta* described by Steinich (1965). Minor differences in the development of the hinge plates are, however, observed as the hinge plates in specimens from Rügen always fuse to form a closed platform (Steinich 1965), while the hinge plates in the specimens from Norfolk form both closed platforms and separate plate-like hinge plates.

Large forms of *A. bronni* (Roemer) differ from *A. coniuncta* in always possessing two distinctly separate concave disc-like hinge plates and a split dorsal median septum.

Occurrence. Overstrand Hotel Lower Mass, Bramerton, Overstrand Hotel Upper Mass 1A, 1, 2 and 2A, Sidestrand 1 and 3A, and Little Marl Point 2. Also known from the Upper Campanian and Maastrichtian of northwest Germany and from the Maastrichtian of East Germany, Denmark and eastern Poland.

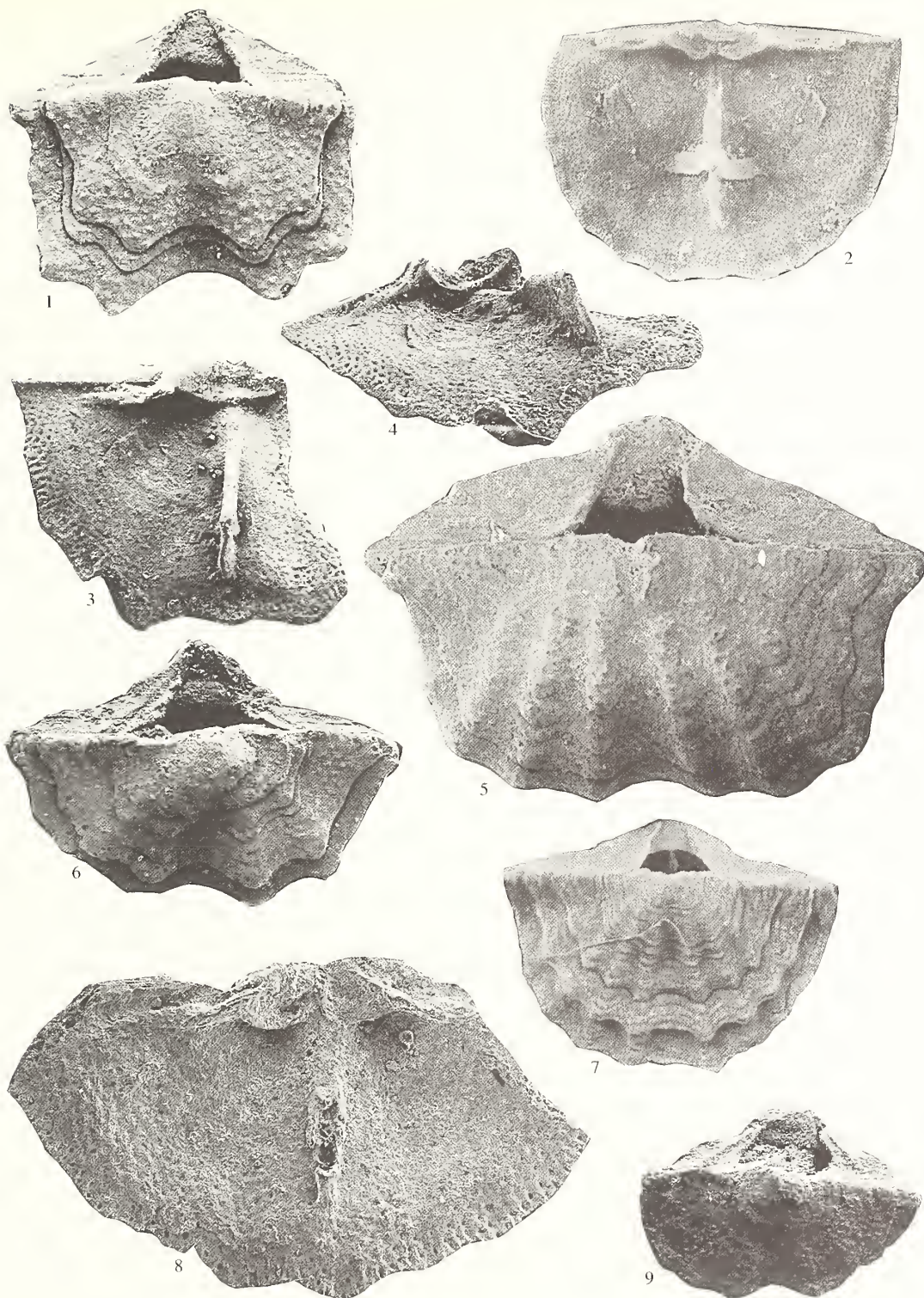
Argyrotheca hirundo (Hagenow, 1842)

Plate 3, figs 6–8

- 1842 *Orthis hirundo* Hagenow, p. 545, pl. 9, fig. 9a–d.
 1965 *Argyrotheca hirundo* (Hagenow); Steinich, p. 152, figs 232–249; pl. 16, fig. 3; pl. 17, fig. 3a–d.
 1972 *Argyrotheca hirundo* (Hagenow); Surlyk, p. 20, figs 5, 17, 18.
 1979 *Argyrotheca hirundo* (Hagenow); Bitner and Pisera, p. 79, pl. 4, fig. 7.
 1982 *Argyrotheca hirundo* (Hagenow); Surlyk, fig. 1, pl. 3, figs f–h.
 1984 *Argyrotheca hirundo* (Hagenow); Surlyk and Johansen, fig. 1.
 1987a *Argyrotheca hirundo* (Hagenow); Johansen, p. 34, fig. 23A–H; pl. 14, figs 1–8.
 1988 *Argyrotheca hirundo* (Hagenow); Johansen, fig. 2, pl. 3, fig. 2.

EXPLANATION OF PLATE 8

Figs 1–4, 7. *Argyrotheca bronni* (Roemer, 1841). 1, MGUH 18232, upper Lower Maastrichtian, Trimingham (coll. WKC, 1971), Norfolk; large juvenile in dorsal view, $\times 30$. 2, SPGIH 3543, lower Lower Maastrichtian, G 147, Krons Moor; interior of large adult dorsal valve, $\times 15$. 3 and 4, MGUH 18233, upper Lower Maastrichtian, Trimingham (coll. WKC, 1971), Norfolk; 3, interior of broken adult dorsal valve, $\times 15$. 4, oblique lateral view showing profile of median septum, $\times 50$. 7, SPGIH 3546, lower Lower Maastrichtian, G 147, Krons Moor; large adult specimen in dorsal view, $\times 10$.
 Figs 5, 6, 8, 9. *Argyrotheca coniuncta* Steinich, 1965. 5, SPGIH 3547, upper Lower Campanian, G 79, Lägerdorf; large adult specimen in dorsal view, $\times 30$. 6, MGUH 18234, upper Lower Maastrichtian, Trimingham (coll. WKC, 1971), Norfolk; juvenile specimen in dorsal view, $\times 25$. 8, MGUH 18235, lowermost Maastrichtian?, Overstrand Hotel Lower Mass, Norfolk; broken adult dorsal valve showing separated hinge plates and high median septum, $\times 25$. 9, MGUH 18236, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 2A, Norfolk; small juvenile in dorsal view, $\times 20$.



Material. Two dorsal valves, one ventral valve, and one fragment. Largest specimen a ventral valve from Bramerton: length, 1.92 mm; width, 1.84 mm; length of dorsal valve (measured from hinge line to anterior margin), 1.28 mm. Catalogue numbers MGUH 16856, 16857; SPGIH 3534.

Description. Outline subtriangular. Shell biconvex with rather flat dorsal valve. Hinge margin enlarged in some specimens as lateral pointed extensions. Surface has very strong growth lines and 4–6 radial ribs in two antero-laterally directed bundles divided by wide median furrow. Beak pointed, suberect, cardinal area plane to slightly concave. Foramen large, triangular, hypothryidid, limited by two narrow deltidial plates. Pedicle collar strongly developed with concave anterior margin. Inner socket ridges strong, anteriorly divergent. Cardinal process knob-shaped. Hinge plates small, converging anteriorly, delimiting a triangular chamber together with socket ridges and cardinal process. Dorsal median septum is high. Its anterior margin forms right angle with inner surface of the shell, posterior margin forms gentle, concave-upward slope. Ventral septum thin, low. Relatively thin shelled.

Remarks. *A. hirundo* is an extremely variable species, but can normally be distinguished by its triangular outline, and the bundled arrangement of the ribs.

Occurrence. Bramerton and Sidestrand 4. Also known from the Upper Campanian and Maastrichtian of northwest Germany and from the Maastrichtian of East Germany, Poland, the Netherlands and Denmark. In Denmark it also occurs in the Lower Danian.

Family TEREBRATELLIDAE King, 1850
Subfamily MAGASINAE Dall, 1870
Genus MAGAS J. Sowerby, 1816

Type species. *Magas pumilus* J. Sowerby, 1816, p. 30.

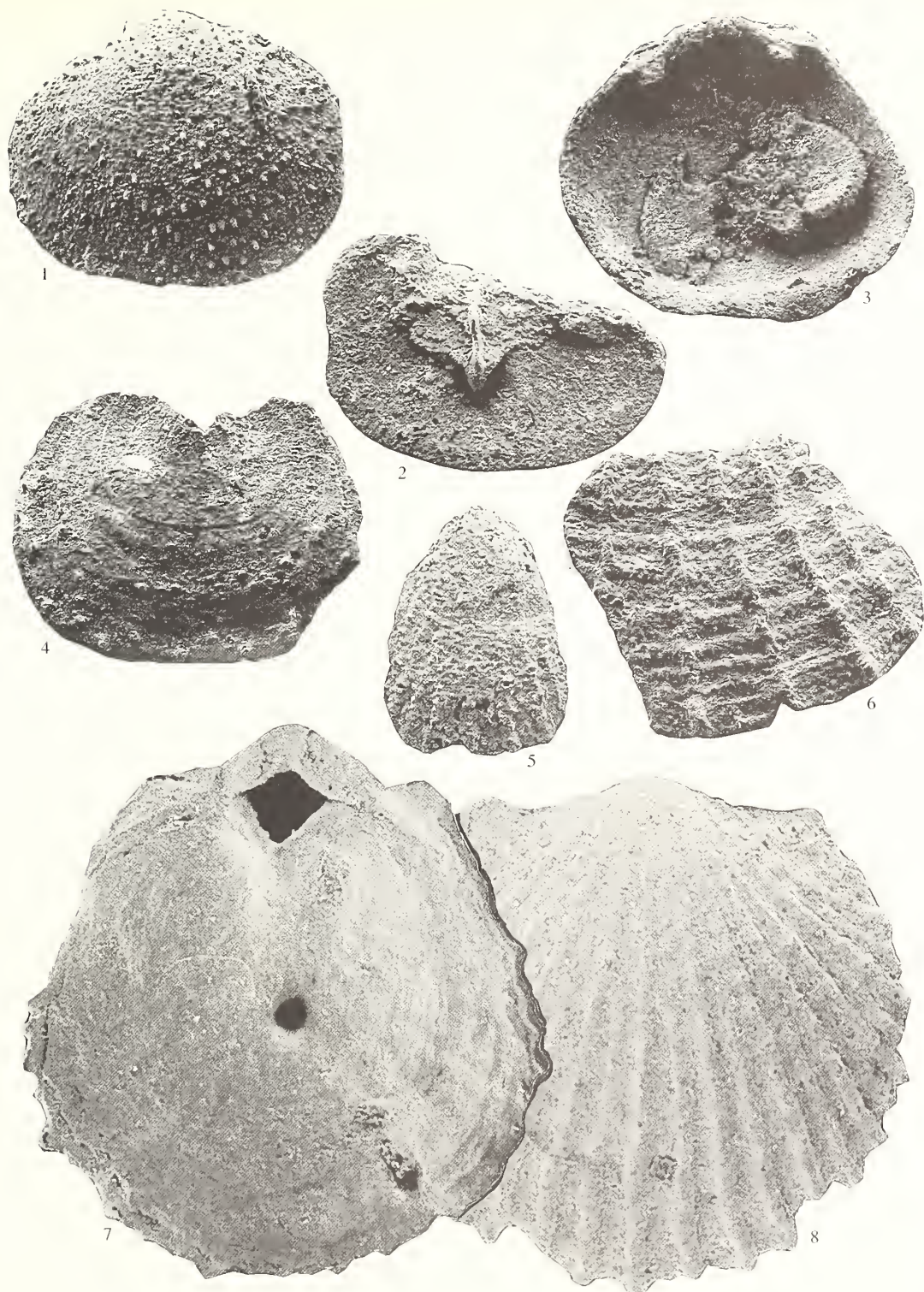
Magas chitoniformis (Schlotheim, 1813)

Plate 10, figs 1–6

- (1798) *Térébratulus fossiles* Faujas, pl. 26, fig. 6.
- 1813 *Terebratula chitoniformis* Schlotheim, p. 133.
- 1818 *Magas pumilus* J. Sowerby, p. 40, pl. 119, figs 3–5.
- 1965 *Magas chitoniformis* (Schlotheim); Steinich, p. 183, figs 280–294; pl. 19, fig. 2; pl. 20, fig. 1a–d.
- 1972 *Magas chitoniformis* (Schlotheim); Surlyk, p. 26, figs 5, 11, 12; pl. 5, fig. c.
- 1982 *Magas chitoniformis* (Schlotheim); Surlyk, fig. 1, pl. 4, figs e–i.
- 1984 *Magas chitoniformis* (Schlotheim); Surlyk and Johansen, fig. 1.
- 1987a *Magas chitoniformis* (Schlotheim); Johansen, p. 43.
- 1988 *Magas chitoniformis* (Schlotheim); Johansen, fig. 2.

EXPLANATION OF PLATE 9

- Figs 1–4. *Aemula inusitata* Steinich, 1968. 1, MGUH 18237, upper Lower Maastrichtian, Trimmingham (coll. WKC, 1971), Norfolk; exterior view of ventral valve, $\times 25$. 2, MGUH 18238, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 3, Norfolk; interior of slightly broken dorsal valve, $\times 20$. 3, MGUH 18239, upper Lower Maastrichtian, Trimmingham (coll. WKC, 1971), Norfolk; interior of ventral valve showing recrystallized schizolophe, $\times 30$. 4, MGUH 18240, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 3, Norfolk; juvenile dorsal valve in exterior, $\times 30$.
- Figs 5–8. *Dracius carnifex* Steinich, 1967. 5, MGUH 18241, lowermost Maastrichtian, Overstrand Hotel Lower Mass, Norfolk; exterior of juvenile ventral valve, $\times 30$. 6, MGUH 18242, lowermost Maastrichtian, Overstrand Hotel Lower Mass, Norfolk; fragment of large ventral valve showing characteristic surface sculpture, $\times 25$. 7, SPGIH 3548, lower Lower Maastrichtian, G 148–150, Kronsnoor; adult specimen in dorsal view, $\times 25$. 8, SPGIH 3549, lower Lower Maastrichtian, G 148–150, Kronsnoor; exterior of large ventral valve, $\times 25$.



Material. Twenty-one complete shells, the majority juvenile specimens, ninety-six dorsal, twenty-seven ventral valves, and one hundred and sixty fragments. Largest specimen a slightly damaged complete adult from Little Marl Point 7: length, 9.0 mm; length of dorsal valve, 7.0 mm; width, 9.0 mm; width of hinge line, 6.4 mm; width of foramen, 1.0 mm and thickness, 4.0 mm. Catalogue numbers MGUH 18243–18246.

Description. Shell relatively large, smooth, with large punctae. Outline changes during growth from elongated oval to subcircular. Shell flattened biconvex in juveniles, becoming plano-convex with very high convex ventral valve as size increases. Hinge line straight, relatively long, giving posterior margin of dorsal valves of juveniles a pair of characteristic shoulders. Beak low, blunt, erect; changes to distinctly incurved during growth. Foramen subtriangular, large, hypothyriddid in juveniles; later triangular, submesothyriddid. Hinge strongly built; brachidium characteristically complex as shown in the illustrations of Steinich (1965, figs 287–292). Dorsal median septum high, strong, ventral valve contains low median ridge in anterior part of valve floor.

Remarks. Juvenile *M. chitoniformis* characteristically possess shoulders on the posterior margin of the dorsal valve but otherwise resemble *Dalligas nobilis* Steinich and *Scumulus inopinatus* Steinich. *D. nobilis* is distinguished from *M. chitoniformis* in possessing a much simpler brachidium. Larger forms of *D. nobilis* bear weak radial ribs; their shells are flat biconvex. *S. inopinatus* differs from juvenile *M. chitoniformis* in often possessing an amphithyriddid foramen and an irregular outline. *Leptothyrellopsis polonicus* Bitner and Pisera is distinguished from juvenile *M. chitoniformis* by its high hypothyriddid foramen and long, high, plate-like median septum.

Occurrence. Keswick, Catton 1, 3 and 3A, Stoke Holy Cross 2?, Catton 4?, 5? and 6?, Caistor 1, Bramerton, Overstrand Hotel Upper Mass 1A, 1, 2, 3 and 4?, Sidestrand 1, 1A?, 3A and 5, Little Marl Point 1A, 1B, 1?, 2, 2A, 3?, 4, 5, 6 and 7, and Trimmingham 1, 2 and 3. Also widely distributed in the Upper Campanian and Maastrichtian of northwest Germany and the Maastrichtian of East Germany, Poland, France, the Netherlands and Denmark.

Subfamily KINGENINAE Elliott, 1948
Genus KINGENA Davidson, 1852

Type species. *Terebratula lima* DeFrance, 1828, p. 156.

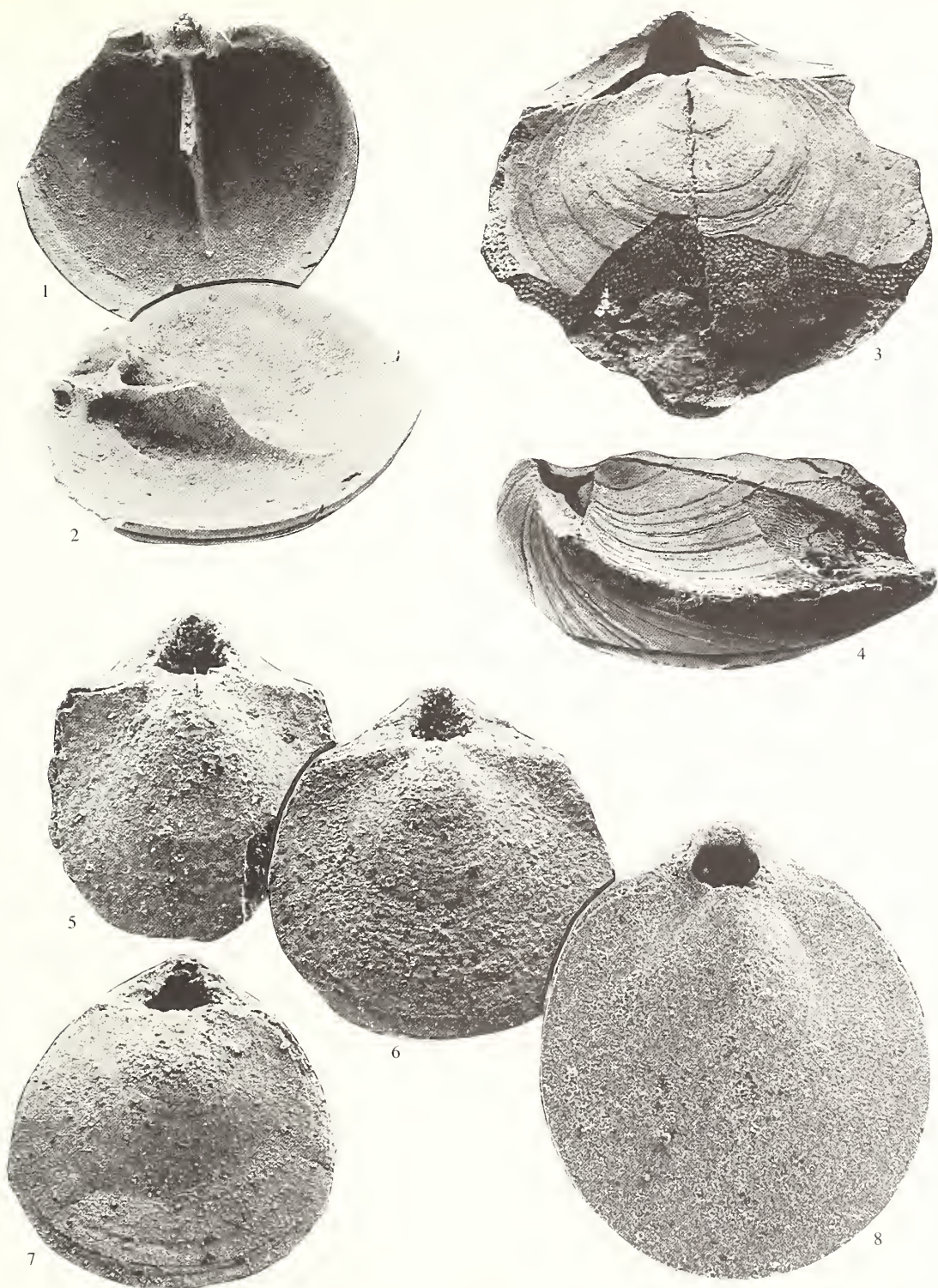
Kingena pentangulata (Woodward, 1833)

Plate 11, figs 5–8

- 1833 *Terebratula pentangulata* Woodward, p. 49, pl. 6, fig. 10.
- 1970 *Kingena pentangulata* (Woodward); Owen, p. 64, pl. 7, figs 6 and 7; pl. 8, figs 2–6; text-fig. 13.
- 1970 *Kingena blackmorei* Owen, p. 63, pl. 7, figs 1–3; pl. 8, fig. 1.
- 1968b *Kingena* sp.; Steinich, p. 342, figs 4 and 5.
- 1972 *Kingena pentangulata* (Woodward); Surlyk, p. 17.

EXPLANATION OF PLATE 10

- Figs 1–6. *Magas chitoniformis* (Schlothheim, 1813). 1 and 2, MGUH 18243, lower Upper Campanian, Catton 1, Norfolk; 1, interior of large slightly broken dorsal valve, $\times 7$. 2, oblique lateral view, $\times 7$. 3 and 4, MGUH 18244, upper Lower Maastrichtian, Little Marl Point 7, Norfolk; 3, slightly broken large adult specimen in dorsal view, $\times 10$; 4, oblique lateral view showing reclining profile, $\times 13$. 5, MGUH 18245, lower Upper Campanian, Catton 3A, Norfolk; small juvenile specimen in dorsal view, $\times 40$. 6, MGUH 18246, lower Upper Campanian, Catton 1, Norfolk; juvenile specimen in dorsal view, $\times 25$.
- Fig. 7. *Dalligas nobilis* Steinich, 1968b, MGUH 18247, lower Upper Campanian, Catton 1, Norfolk; adult specimen in dorsal view, $\times 25$.
- Fig. 8. *Scumulus inopinatus* Steinich, 1968b, SPGIH 3550, lower Upper Campanian, G 109, Lägerdorf; adult specimen in dorsal view, $\times 30$.



- 1979 *Kingena* sp.; Bitner and Pisera, p. 81, pl. 5, figs 1 and 2.
 1984 *Kingena pentangulata* (Woodward); Surlyk and Johansen, fig. 1.
 1987a *Kingena pentangulata* (Woodward); Johansen, p. 42, pl. 20, figs 5 and 6.
 1988 *Kingena pentangulata* (Woodward); Johansen, fig. 2.

Material. Seven shells, thirty-seven dorsal, thirty-four ventral valves, and two hundred and fifty-six fragments. Largest valves have following dimensions: fragment of ventral valve from Overstrand Hotel Upper Mass 2A: length at least 4.4 mm; dorsal valve from Cley: length, 2.9 mm; width, 3.4 mm; shell from Overstrand Hotel Upper Mass 3: length, 2.6 mm; width, 3.0 mm; length of dorsal valve, 2.2 mm; thickness at least 0.6 mm. Catalogue numbers MGUH 18252–18255.

Description. Adults not seen; medium-sized specimens are highly fragmented. Juvenile stages less than 5 mm in length. The outline changes during growth from subtriangular to circular to subpentagonal. Small forms plano-convex to weakly biconvex; larger forms more uniformly biconvex. Commissure straight in early stages. Shell surface characteristically bears densely-spaced small regular tubercles. Beak almost straight to suberect in earliest stages, changing to suberect and finally erect. Cardinal area wide, sharply delimited. Foramen large, trapezoidal; submesothyridid in forms less than 5 mm long. It becomes permesothyridid as beak becomes more incurved in larger forms. Foramen limited laterally by rather large triangular deltidial plates. Teeth strong, pointed, supported by well-developed dental plates which converge posteriorly. Larger specimens have well-defined hinge plate. A low median septum is formed at c. 0.8 mm length. At c. 1.4 mm length two pointed antero-laterally directed ascending branches form at top of anterior margin of the septum. At the same time two short crurae are formed as extensions of inner socket ridges. Strongly divergent descending branches extend from end of crurae. Latest stages of brachidium development not seen in present material. Shell is thin and almost always rather deformed. Inner surface is smooth.

Remarks. The present material is referred to *K. pentangulata* with slight reservation. It corresponds, however, in all details to abundant material of this species from the Danish Maastrichtian. Furthermore the neotype of *K. pentangulata* (Woodward) selected by Owen (1970) comes from the transition between the Eaton and Weybourne Chalk Members in Norfolk, while its closest relative *K. blackmorei* Owen is said to characterize the somewhat older chalk of the *Goniotheuthis quadrata* Zone in South Wiltshire and Hampshire (Owen 1970). The differences between the two species are extremely slight, and mainly reflect one main feature, the less incurved umbo of *K. blackmorei*. We prefer to include *K. blackmorei* in *K. pentangulata*.

The surface sculpture, hinge plate and brachidium distinguish *K. pentangulata* from all other known Upper Campanian–Maastrichtian species.

Occurrence. Cley, Keswick, Catton 1, 3, 3A, 4, 5 and 6, Caistor 3 and 1, Whitlingham, Overstrand Hotel Lower Mass, Bramerton, Overstrand Hotel Upper Mass 1A, 1, 2, 2A, 3 and 4, Sidestrand 1, 1A, 2, 3, 3A and 4, and Little Marl Point 1A. The species is known from the Upper Campanian–Maastrichtian and possibly older Chalk strata of northwest Europe.

Family PLATIDIINAE Thomson, 1927
 Genus AEMULA Steinich, 1968

Type species. *Aemula inusitata* Steinich, 1968a, p. 193.

Aemula inusitata Steinich, 1968

Plate 9, figs 1–4

- 1968a *Aemula inusitata* Steinich, p. 192, figs 1–5; pl. 1, fig. 1.
 1972 *Aemula inusitata* Steinich; Surlyk, fig. 5, pl. 3, figs e, f, h.
 1974 *Aemula inusitata* Steinich; Surlyk, figs 1 and 3, pl. 2.
 1979 *Aemula inusitata* Steinich; Bitner and Pisera, p. 79, pl. 5, fig. 4.
 1982 *Aemula inusitata* Steinich; Surlyk, fig. 1, pl. 2, figs g and h.
 1984 *Aemula inusitata* Steinich; Surlyk and Johansen, fig. 1.

1987a *Aemula inusitata* Steinich; Johansen, p. 39, pl. 18, figs 1–5.

1988 *Aemula inusitata* Steinich; Johansen, fig. 2, pl. 3, figs 4a, b, 5, 6.

Material. Five complete shells, ten dorsal, sixty-three ventral valves and ten fragments. Largest specimen is a dorsal valve from Overstrand Hotel Upper Mass 3: length, 2.32 mm; width, 2.64 mm. Catalogue numbers MGUH 18237–18240.

Description. Outline oval to circular, commonly very irregular. Shell plano-convex to slightly concavo-convex. Commissure straight in regular specimens. Surface of dorsal valve smooth, surface of the ventral valve bears short pointed tubercles. Shells with width of less than 1.0 mm rarely have tubercles, but larger specimens show no correlation between shell size and size and density of tubercles. There are several growth lines, clearly developed on the dorsal valve. Beak very short, suberect. Cardinal area small, clearly delineated. Hinge line almost straight. Foramen relatively large, amphithyridid; laterally delineated by two narrow deltidial plates. Short, slightly elevated pedicle collar is delineated from deltidial plates by furrow. Teeth are very short, obtuse. Inner socket ridges well-developed, extending somewhat outside posterior shell margin. Dorsal valve has low triangular median septum, with two ventrally directed short triangular ascending branches. *A. inusitata* has a strongly developed spicular skeleton; schizolophe. Inner side of the rather thin shell is smooth.

Remarks. *A. inusitata* is easily distinguished from all other Chalk brachiopods. Very regular and smooth forms may, however, show considerable overlap with a new species of *Aemula* illustrated from the Maastrichtian chalk of Hemmoor, northwest Germany by Surlyk (1974, pl. 2b). The present material does not help in the separation of the two forms.

Occurrence. Keswick, Caistor 1, Overstrand Hotel Lower Mass, Bramerton, Overstrand Hotel Upper Mass 1A, 2, 2A, 3 and 4, Sidestrand 3, 3A, 4 and 5, and Little Marl Point 1B, 6 and 7. Also known from the Santonian to the Maastrichtian of northwest Germany and from the Maastrichtian of East Germany, Denmark and eastern Poland.

Aemula sp.

Material. One complete shell and one ventral valve. Both specimens are juveniles with shell widths around 1.5 mm.

Description. Shell smooth, thin, plano-convex pointed, oval, slightly irregular outline. Beak very short, acute, suberect; foramen large, amphithyridid. Teeth small, blunt, inner socket ridges protrude beyond posterior shell margin. Internal morphology not known.

Remarks. *A. inusitata* Steinich differs from this species in possessing a shell sculpture of low, densely-spaced tubercles concentrated on the ventral valve. This smooth *Aemula* sp. may be conspecific with the *Aemula* n. sp. illustrated from the Maastrichtian chalk of Hemmoor, northwest Germany (Surlyk, 1974, pl. 2b). The material from Norfolk is, however, too small to allow this problem to be resolved.

Occurrence. Caistor 1.

Genus SCUMULUS Steinich, 1968

Type species. *Scumulus inopinatus* Steinich, 1968a, p. 199, pl. 1, fig. 2.

Scumulus sp.

Material. One fragmented ventral valve is present, but this is not illustrated here due to its poor state of preservation. For comparison a specimen of *S. inopinatus* from the lower Upper Campanian of Lägerdorf is shown (Pl. 10, fig. 8). Catalogue number SPGIH 3550.

Description. Valve small, smooth, elongated oval in outline. Beak short, erect, blunt; area characteristically broad and triangular with lateral edges formed by shallow ridges. Deltidial plates very narrow, hinge teeth are strong, acute.

Remarks. The species can be assigned to the genus *Scumulus* Steinich, but the material does not allow specific determination.

Juveniles of *Magas chitoniformis* (Schlotheim) show great resemblance to this species, but *M. chitoniformis* differs in possessing a small, distinctly limited cardinal area and large punctae. *Leptothyrellopsis polonicus* Bitner and Pisera and *Dalligas nobilis* Steinich both differ from the Norfolk species in their very narrow cardinal areas.

Occurrence. Caistor 1.

Family DALLINIDAE Beecher, 1893

Genus DALLIGAS Steinich, 1968

Type species. *Dalligas nobilis* Steinich, 1968b, p. 336, pl. 1, fig. 1.

Dalligas nobilis Steinich, 1968

Plate 10, fig. 7

1968b *Dalligas nobilis* Steinich, p. 336, figs 1–3; pl. 1, figs 1 and 2.

1972 *Dalligas nobilis* Steinich; Surlyk, p. 20, figs 5, 13–15, 17, 18.

1987a *Dalligas nobilis* Steinich; Johansen, p. 43, pl. 18, figs 6 and 7.

Material. Two bivalved specimens, three ventral and one dorsal valve. All specimens fragmentary, largest specimen, from Overstrand Hotel Upper Mass 4, is 2.8 mm long. Catalogue number MGUH 18247.

Description. Outline circular, shell flatly biconvex. Auricles not delimited. Commissure straight. Numerous very fine radial ribs appear at 0.5–1.0 mm width. Rib number about 30. Cardinal area is narrow, triangular. Deltidial plates narrow, well-separated posteriorly. Foramen triangular to trapezoidal. Pedicle collar wide, well-defined. Inner socket ridges subparallel, forming characteristic triangular area together with well-defined hinge plates, and posterior margin of the median septum. Septum high, bearing two short ascending branches. Remaining elements of the brachidium not developed. Shell relatively thin.

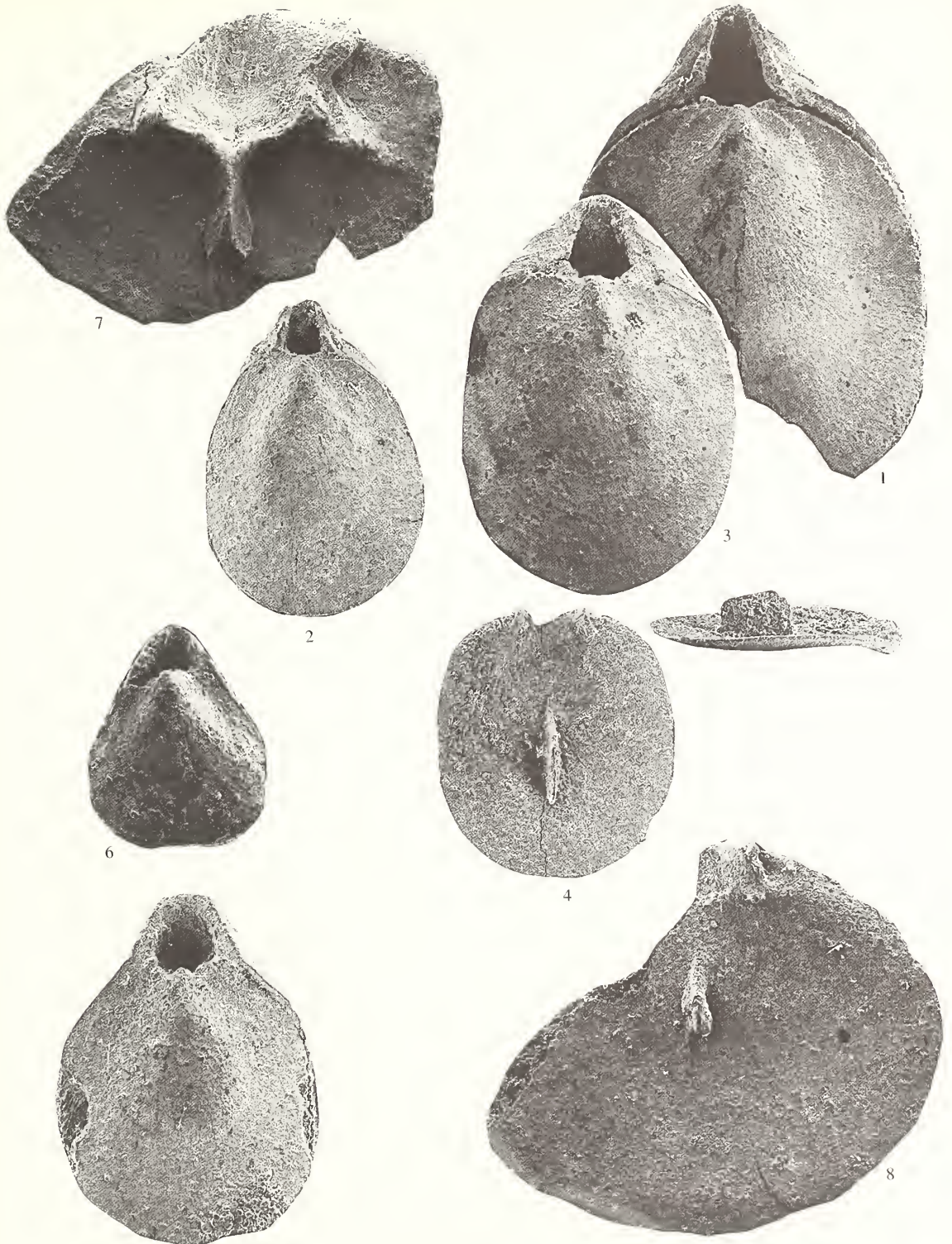
Remarks. The specimen closely resembles *D. nobilis* as described by Steinich (1968b) from Rügen, although the ribbing seems to appear somewhat earlier in ontogeny. Juvenile specimens, where ribbing has not yet developed, cannot be distinguished from the smooth *D. mielnicensis* Bitner and Pisera. Young specimens differ from *Leptothyrellopsis polonicus* Bitner and Pisera in their more circular outline, larger foramen, triangular area and wider, less pointed beak.

Occurrence. Keswick, Catton 1, Overstrand Hotel Lower Mass, and Overstrand Hotel Upper Mass 2A and 4. The stratigraphic and geographic distributions of this almost featureless species are not yet well known.

EXPLANATION OF PLATE 11

Figs 1–5. *Leptothyrellopsis polonicus* Bitner and Pisera, 1979. 1, MGUH 18248, lower Lower Maastrichtian, Sidstrand 3A, Norfolk; broken adult specimen in dorsal view, $\times 30$. 2, MGUH 18249, uppermost Campanian?, Whitlingham, Norfolk; juvenile in dorsal view, $\times 25$. 3, MGUH 18250, uppermost Campanian?, Whitlingham, Norfolk; large juvenile specimen in dorsal view, $\times 30$. 4 and 5, MGUH 18251, lower Lower Maastrichtian, Sidstrand 2, Norfolk; 4, interior of juvenile dorsal valve, $\times 25$; 5, 4 in lateral view showing profile of median septum, $\times 50$.

Figs 6–9. *Kingena pentangulata* (Woodward, 1833). 6, MGUH 18252, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 2A, Norfolk; cardinal area of medium-sized dorsal valve, $\times 25$. 7, MGUH 18253, lower Lower Maastrichtian, Overstrand Hotel Upper Mass 2A, Norfolk; small juvenile specimen in dorsal view, $\times 25$. 8, MGUH 18254, upper Upper Campanian, Caistor 3, Norfolk; interior of broken medium-sized dorsal valve, $\times 25$. 9, MGUH 18255, upper Upper Campanian, Catton 3A, Norfolk; juvenile specimen in dorsal view, $\times 30$.



Family THECIDEIDAE Gray, 1840
 Subfamily LACAZELLINAE Backhaus, 1959
 Genus LACAZELLA Munier-Chalmas, 1880

Type species. Thecidea mediterranea Risso, 1826, p. 393.

Subgenus BIFOLIUM Elliott, 1948

Lacazella (Bifolium) wetherelli (Morris, 1851)

Plate 1, fig. 7

- 1851 *Thecidea wetherelli* Morris, p. 86, pl. 4, figs 1–3.
- 1852 *Thecidea wetherelli* Morris; Davidson, p. 14, pl. 1, figs 15–26.
- 1874 *Thecidium wetherelli* Morris; Davidson, p. 22.
- 1908 *Thecidium wetherelli* Morris; Rowe, p. 320.
- 1959 *Lacazella (Bifolium) wetherelli* (Morris); Backhaus, p. 35, pl. 2, figs 1–3.
- 1965 *Lacazella (Bifolium) wetherelli* (Morris); Steinich, p. 15, pl. 4, figs 2 and 3a, b.
- 1972 *Bifolium wetherelli* (Morris); Surlyk, p. 27, fig. 5.
- 1974 *Praelacazella wetherelli* (Morris); Pajaud, p. 333.
- 1988 *Lacazella (Bifolium) wetherelli* (Morris); Johansen, fig. 2.

Material. Four dorsal valves and three fragments, all of which probably belong to ventral valves. Largest specimen a dorsal valve from Lower Maastrichtian sample Little Marl Point 1B. Length of dorsal valve, 5.5 mm; width, 6.5 mm. Catalogue number MGUH 16846.

Description. Outline of the dorsal valve subtriangular to trapezoidal. Shell margins broad, steep, levelling out towards anterior shell margin. Valves thick, stout. Shell surface smooth with several growth rings. Dorsal valve planar. Shell margin sculptured with numerous fine, minute pustules and radiating, low ridges. Posterior shell margin short, straight. Cardinal process protrudes well beyond posterior shell margin and is broad and short. Ascending part of brachial apparatus consists of two separate laminae which rise anteriorly in dorsal valve. Laminae follow depression in floor of valve and run obliquely posteriorly towards jugum, where laminae abruptly change direction of growth deflecting towards aperture. Folded laminae unite mid dorsally above jugum. A second folding of laminae may occur but characteristically only one or two folds are present. Ptycholophe.

Remarks. Backhaus (1959) mentions that the dorsal valve of this species is typically very thin, but this is not the case in the specimens from Norfolk. When present, the ventral valve of this species is characterized by being attached (cemented) to the substrate with the entire outer surface, and by possessing a distinct radial rib pattern in the inner surface of the ventral valve. *Lacazella (Bifolium) wetherelli* is distinguished from other closely-related species of *Lacazella* in the form of the brachial apparatus. In *L. (B.) wetherelli* the laminae are folded once or in some cases twice.

Occurrence. Little Marl Point 1B, 1, 4 and 7?. Also known from Upper Campanian–Maastrichtian Chalk strata of northwest Germany and from the Maastrichtian of East Germany and Denmark.

Family UNCERTAIN
 Genus LEPTOTHYRELLOPSIS Bitner and Pisera, 1979

Type species. Leptothyrellopsis polonicus Bitner and Pisera, 1979, p. 82, pl. 7, fig. 2.

Leptothyrellopsis polonicus Bitner and Pisera, 1979

Plate 11, figs 1–4

- 1979 *Leptothyrellopsis polonicus* Bitner and Pisera, p. 82, pl. 7, figs 1–4.
- 1982 *Leptothyrellopsis polonicus* Bitner and Pisera; Surlyk, fig. 1, pl. 3, figs c–e.
- 1988 *Leptothyrellopsis polonicus* Bitner and Pisera; Johansen, fig. 2.

Material. Seventy complete shells, one hundred and ninety dorsal, one hundred and fifty-three ventral valves, and fifty-eight fragments. Largest specimen from Cley: length, 3.4 mm; width, 2.8 mm; length of brachial valve, 2.9 mm; thickness, 0.6 mm. Catalogue numbers MGUH 18248–18251.

Description. Outline oval to elongate oval. No clearly delimited auricles. Shell flatly biconvex; commissure straight. Surface smooth apart from a few growth lines; beak erect; shell is punctate; area small; deltidial plates narrow with subparallel sides; elevated above shell surface as low ridges. Foramen large, subtriangular. There is no pedicle collar but high inner socket ridges. Dorsal valve has prominent plate-like median septum.

Remarks. The almost total absence of diagnostic features makes it difficult to distinguish *L. polonicus* from other small smooth brachiopods. It differs from juvenile *Dalligas* Steinich and *Magas chitoniformis* (Schlotheim) in the absence of a pedicle collar and of a prominent hinge plate. *Scumulus inopinatus* Steinich can be distinguished from *L. polonicus* by its well-developed brachidium, its amphithyridid foramen and irregular outline.

Occurrence. Cley, Keswick, Catton 3A, 5 and 6, Caistor 1, Whitlingham, Overstrand Hotel Lower Mass, Overstrand Hotel Upper Mass 1A, 1, 2, 2A, 3 and 4, Sidestrand 1, 1A, 2, 3A and 4, Little Marl Point 1B, 2 and 3, Trimingham 1, and Little Marl Point 4 and 6. This species is known from Upper Campanian–Maastrichtian Chalk strata of northwest Germany, and from the Maastrichtian of eastern Poland and probably also Denmark.

SUMMARY

The Upper Cretaceous Chalk of Norfolk is not very well known due to its poor exposure in scattered, commonly abandoned chalk pits, and in glacially transported masses exposed in coastal cliffs. The sediments consist of white to yellowish chalk with scattered bands of nodular or barrel-shaped flints ('paramoudras'). Calcarenites, nodular cemented chalks with sponge impressions, and hardgrounds are also common.

The Chalk has been subdivided into a number of units, but the stratigraphic nature of these is rather vague, although they seem to be mainly palaeontologically defined (see also Peake and Hancock 1961, 1970; Wood 1988). In the present paper we have attempted to present a coherent lithostratigraphic scheme based on the older units, and eight lithostratigraphical units of member rank are proposed.

A detailed biozonation based on the micromorphic brachiopod fauna has been established for the Upper Campanian and Maastrichtian of northwest Europe (Surlyk 1984). A large number of bulk samples collected in the Upper Campanian–Lower Maastrichtian of Norfolk, England has, after Glauber-Salt treatment and freeze-thawing, yielded a brachiopod fauna of about 2200 specimens representing at least thirty-five species. All of the species present are known also from the Upper Cretaceous Chalk of Denmark, Sweden, Germany and Poland.

The existence of this fauna in the English Chalk makes it possible to correlate parts of the Campanian and Maastrichtian outcrops in Norfolk with more complete and better exposed sections of northwest continental Europe, especially the Campanian–Maastrichtian boundary section at Kronsnoor, West Germany.

In spite of the condensed and poorly exposed nature of the Norfolk section, most of the brachiopod zones established in northwest Europe can be recognized. These zones are from below:

1. the *tenuicostata-longicollis* Zone corresponding to the bulk of the Upper Campanian of Norfolk;
2. the *longicollis-jasmundi* Zone corresponding to the uppermost Upper Campanian;
3. the *acutirostris-spinosa* Zone corresponding to the basal Maastrichtian;
4. the *spinosa-pulchellus* Zone corresponding to the middle part of the Lower Maastrichtian;
5. the *pulchellus-pulchellus* Zone of the upper Lower Maastrichtian.

The *jasmundi-acutirostris* Zone which includes the lowermost Maastrichtian in Kronsnoor is undoubtedly represented in unexposed strata between the highest Campanian locality, Whitlingham and the lowest Maastrichtian exposed at Overstrand Hotel Lower Mass.

In spite of its highly fragmentary exposure, the Upper Campanian–Maastrichtian of Norfolk is now correlated in detail on the basis of the brachiopods with the standard boundary sequences at Krons Moor and Lägerdorf in northwest Germany, and with the detailed macrofossil zonation established for these localities by German workers.

Acknowledgements. The samples which form the basis for the present study were collected in 1971 by W. Kegel Christensen and F. Surlyk under the excellent and highly inspiring guidance of J. M. Hancock and N. B. Peake. Some additional samples were collected by R. G. Bromley in 1971. This paper was read critically by J. M. Hancock, N. B. Peake, W. J. Kennedy and one anonymous referee. The typing was done by B. Larsen and A. Brantsen and drafting by B. Sikker Hansen. Stereoscan work was undertaken in the Scanning Electron Microscope Laboratory of the Geological Central Institute, University of Copenhagen, and darkroom work was done by J. Aagaard and O. B. Berthelsen. The paper was written while Surlyk was a recipient of a research professorship awarded by the Danish Natural Science Research Council.

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Typescript received 3 July 1989

Revised typescript received 5 February 1990

VERTEBRATES FROM THE MIDDLE TRIASSIC OTTER SANDSTONE FORMATION OF DEVON

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ABSTRACT. New vertebrate material from the Otter Sandstone Formation of Devon includes a cleithrolepidid fish, temnospondyl amphibians, a procolophonid reptile, and a tooth which may be attributed to a tanystropheid reptile. The Cleithrolepididae is represented by several specimens of *Dipteronotus cyphus*. The temnospondyl amphibian material includes two skull roof fragments referable to *Mastodonsaurus lavisi*, a skull and fragments assignable to the benthosuchid *Eocyclotosaurus* sp., and one mandibular fragment of an indeterminate large capitosaurid. The procolophonid material comprises several tooth-bearing fragments and a partial interclavicle, and appears to represent a relatively primitive form. A single tricuspid tooth most closely resembles those of the reptile *Tanystropheus*. An enigmatic elongate bone may be the neural spine of a *Ctenosauriscus*-like thecodontian or the rib of a dicynodont therapsid. No fish, capitosaurid, or procolophonid material has previously been described from the Otter Sandstone, and the benthosuchid *Eocyclotosaurus* has not previously been identified in the Triassic of the British Isles. Comparison of this vertebrate assemblage with those of Western and Central Europe and North America supports an Anisian age for the Otter Sandstone.

THE Otter Sandstone Formation is exposed along the south-east coast of Devon from Otterton Point near Budleigh Salterton to Port Royal, east of Sidmouth. It is a 118 metre thick Triassic sequence of largely fluvatile sandstones with included breccias and thin mudstone layers. It overlies the Budleigh Salterton Pebble Beds and is in turn overlain by 'marls' of the Mercia Mudstone Group. Warrington *et al.* (1980) and Laming (1982) reviewed the stratigraphy of the British Triassic and discussed the problems of correlating the Otter Sandstone with other Triassic sequences. The Otter Sandstone has proved difficult to date as it includes no volcanic rocks, and attempts to obtain spores have not been successful (Warrington 1971, and pers. comm. to M.A.T. 1984). The discontinuity at the base of the Budleigh Salterton Pebble Beds is usually taken as the base of the local Triassic, while palynomorphs have provided evidence for a Carnian (late Triassic) age for beds 135 m above the base of the Mercia Mudstone Group (Warrington 1971). The only evidence for a more precise dating of the Otter Sandstone Formation is the fossil vertebrates found within it.

In the nineteenth century, vertebrate material was collected from coastal exposures of the Otter Sandstone in two localities at least. Whitaker (1869) recovered a rhynchosaur specimen (GSM 90494) from a 'brecciated horizon' in the lower part of the Otter Sandstone Formation exposed in a low cliff on the west bank of the mouth of the River Otter. Later workers (Johnston-Lavis 1876; Metcalfe 1884; Carter 1888) found material of amphibians, reptiles, and coprolites (all BMNH) from fallen blocks ascribed to an 'ossiferous zone... ten feet from the top of the Sandstone' near High Peak, west of Sidmouth. Recently a large collection of vertebrate material (all EXEMS) has been made by Mr P. S. Spencer, principally from the north-eastern region of the exposure from Smallstones Point towards Sidmouth (Spencer and Isaac 1983, fig. 1) but also from a scattering of localities from Danger Point near the mouth of the Otter River eastwards to Port Royal at the mouth of the River Sid. Spencer and Isaac confirmed the early impression that the upper part of the Otter Sandstone is the most fossiliferous, specifying the top 20 m or so. A few specimens have been found *in situ*, but most have been recovered from fallen blocks and cannot be readily attributed to a specific horizon within the cliff section. Spencer and Isaac (1983) gave a preliminary account of the material which has now been subject to more detailed study. The rhynchosaur material has been described by Dr M. J. Benton (Bristol University) (Benton 1987, 1990), while much of the

remaining new fish, amphibian and reptile material is described in the following account. Following the systematic description of this material, the age of the Otter Sandstone Formation is discussed.

Institutional abbreviations used in this work are: BMNH, British Museum (Natural History), London; EXEMS, Royal Albert Memorial Museum, Exeter, Devon; GSM, British Geological Survey, Keyworth, Nottinghamshire; NMI, National Museum of Ireland, Dublin; SMNS, Staatliches Museum für Naturkunde, Stuttgart; WARMS, Warwick County Museum, Warwickshire (WCM in earlier literature).

SYSTEMATIC PALAEOLOGY

Class OSTEICHTHYES
 Subclass ACTINOPTERYGII
 Infraclass ACTINOPTERI
 Superdivision NEOPTERYGII
 Plesion PERLEIDIFORMES
 Family CLEITHROLEPIDIDAE Wade, 1935
 Genus DIPTERONOTUS Egerton, 1854

Type species. Dipteronotus cyphus Egerton, 1854

Emended diagnosis. Deep-bodied fish in which the dorsal side is marked with a hump. Scaling characteristic, with fewer scales below lateral line than above it, and with extremely enlarged and pointed dorsal ridge scales between skull and dorsal fin. Head much deepened posteriorly, frontals greatly enlarged, and suspensorium upright. Orbit large, and two supraorbitals. Preoperculum vertical with a prominent pit-line ventrally and an infraorbital process which extends behind the triangular maxillary. Body lobe of tail reduced, rays 12–16 with expanded bases.

Remarks. Prominent dorsal ridge scales midway between the skull and dorsal fin are confined to *Pseudobeaconia* and *Dipteronotus* among cleithrolepidids. In *D. cyphus* they were originally mistaken for the bases of fin-rays (Egerton 1854, p. 369). Two further species of *Dipteronotus* have subsequently been described, namely: *D. aculeatus* from the Upper Buntsandstein (Scythian-Anisian) of France and Germany (Jörg 1969; Gall *et al.* 1974) and *D. gibbosus* from the Upper Triassic of Morocco (Martin 1980). These two species appear to be immediately related and together they form the sister-taxon to *D. cyphus* (Gardiner 1988).

Dipteronotus cyphus Egerton, 1854

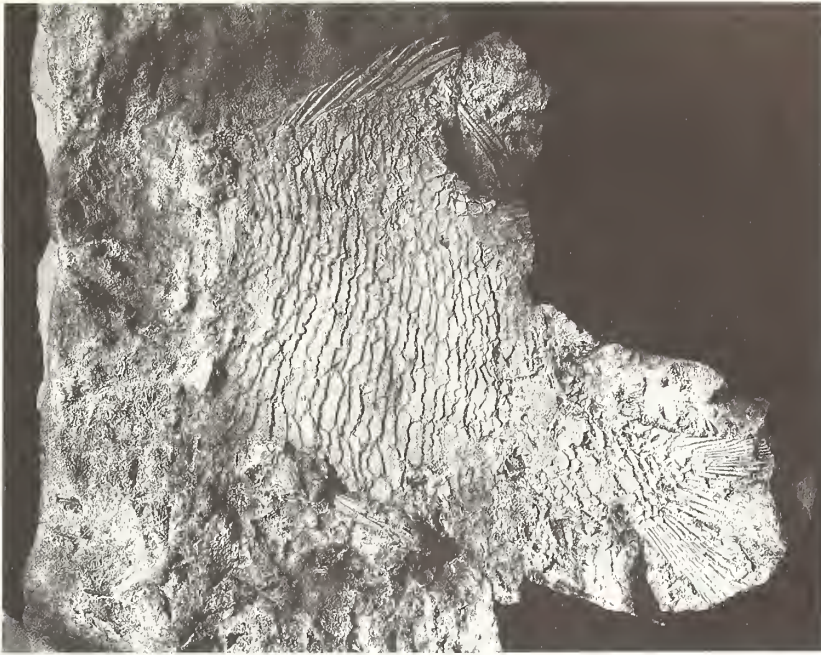
Text-fig. 1

- 1854 *Dipteronotus cyphus* Egerton, p. 369, pl. 11, figs 1 and 2.
- 1910 *Dipteronotus cyphus* Egerton; Woodward, p. 322.
- 1973 *Dipteronotus cyphus* Egerton; Hutchinson, p. 321.
- 1974 *Dipteronotus cyphus* Egerton; Gall *et al.*, pp. 7–8, pl. 5.

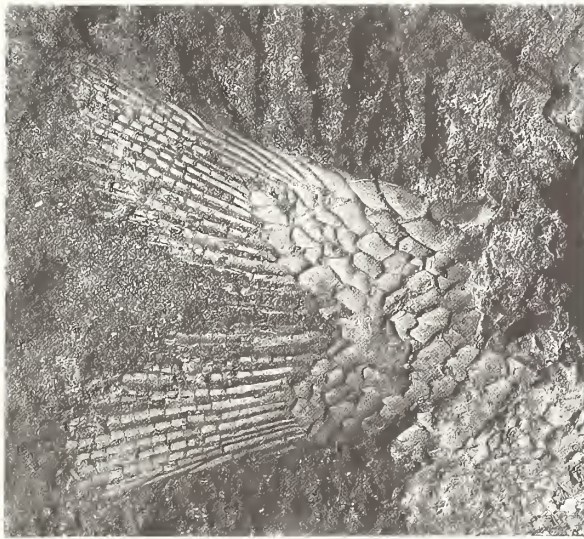
Holotype. GSM 18188 and 18189, counterparts of an almost complete specimen, from the Bromsgrove Sandstone Formation, Middle Triassic of Bromsgrove, Hereford and Worcester (previously Worcestershire).

Referred material. NMI F.15677, a small fragment of body from the type locality. EXEMS 60/1985.293 and 294, two partial specimens in a fine mudstone from the Otter Sandstone Formation (Text-fig. 1). These specimens are better preserved than the holotype and have permitted a more accurate count to be made of the various fin-rays as well as a more detailed description of the scale ornamentation. Further specimens were collected and are in the EXEMS collection.

Emended diagnosis (based on holotype and EXEMS 60/1985.293 and 294). A *Dipteronotus* with



A



B

TEXT-FIG. 1. *Dipteronotus cyphus* Egerton. A, EXEMS 60/1985.293, entire specimen, $\times 1.5$. B, EXEMS 60/1985.294, detail showing caudal fin, $\times 3$.

10–13 elongate, spinose, ridge scales in front of dorsal fin; ventral ridge scales similar, but smaller than dorsals. Dorsal fin comprising 17 rays and 5 basal fulcra, and anal fin with about 14 rays and 2 fulcra. Tail with 27–30 rays of which the most dorsal 12 are epaxial and with three prominent basal fulcra dorsally and ventrally; pelvic fin with 5–6 rays. Dermosphenotic tall and narrow, and 2 infraorbitals. A single suborbital probably present between top of preoperculum and dermosphenotic. Scales with posterior crimping, those on dorsal hump having several rows of

backwardly-pointing tubercles. On rest of body, scales are pectinate posteriorly with some ten projections.

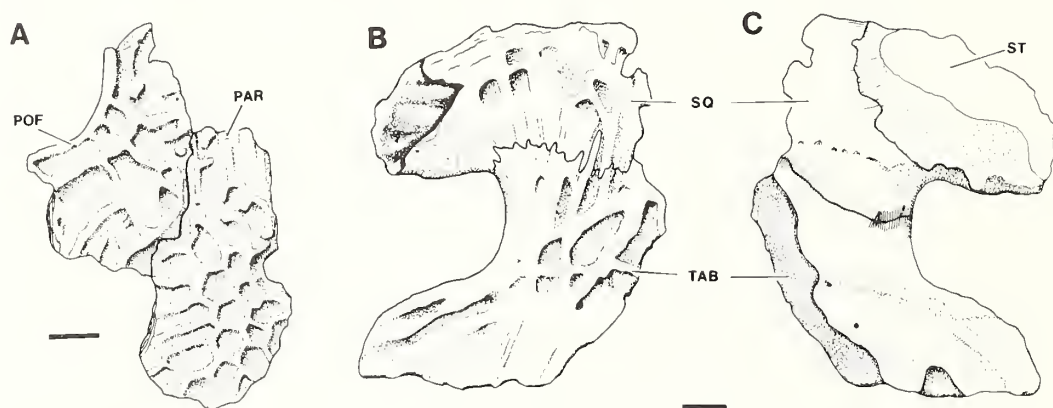
Class AMPHIBIA
Order TEMNOSPONDYLII
Family MASTODONSAURIDAE Lydekker, 1885
Genus MASTODONSAURUS Jaeger, 1828

Type species. Salamandroides giganteus Jaeger, 1828

Mastodonsaurus lavisi (Seeley) Paton, 1974 *nomen dubium*

Text-fig. 2A-C

- 1876 *Labyrinthodon lavisi* Seeley, p. 278, pl. 19, figs 1-3.
- 1916 *Labyrinthodon lavisi* Seeley; Wills, p. 15.
- 1947 '*Labyrinthodon*' *lavisi* Seeley; Romer, p. 228.
- 1962 '*Labyrinthodon*' *lavisi* Seeley; Watson, p. 252.
- 1965 *Labyrinthodon lavisi* Seeley; Welles and Cosgriff, p. 35 as a *nomen vanum*.
- 1974 *Mastodonsaurus lavisi* (Seeley); Paton, p. 282, figs 14B and 16B.



TEXT-FIG. 2. *Mastodonsaurus lavisi* (Seeley). A, EXEMS 60/1985.287, left postfrontal and parietal. B, C, EXEMS 60/1985.309, left tabular, squamosal and part of supratemporal in (B) dorsal and (C) ventral view. Abbreviations for Text-figs 2-4: FR, frontal; L, lacrimal; J, jugal; PAR, parietal; PO, postorbital; POF, postfrontal; PP, postparietal; PRF, prefrontal; QJ, quadratojugal; SQ, squamosal; ST, supratemporal; TAB, tabular. Scale bars, 10 mm.

Holotype. BMNH R.4215, posterior region of right mandible, collected by H. J. Johnston-Lavis from the Otter Sandstone Formation below High Peak, west of Sidmouth, Devon (Johnston-Lavis, 1876). Most recently figured by Paton (1974, figs 14B and 16B).

Remarks. Up to 1974, the specific name *lavisi* was restricted to a mandibular fragment from the Otter Sandstone. Paton (1974) revised the British Triassic temnospondyl material and combined the Midlands and Devon mastodonsaurid specimens as one species for which the senior specific name was *lavisi* borne by this specimen. The following description is restricted to Otter Sandstone specimens and unity of the Midlands material with *M. lavisi* is not assumed, although some comparison is made with specimens from Warwickshire.

Diagnosis. No species-level diagnosis can be given for the Otter Sandstone *Mastodonsaurus*. Paton's

(1974) diagnosis of *M. lavisi* is based on *Mastodonsaurus* generic characters which permit it to be distinguished only from contemporaneous capitosaurid material. Pending a revision of the species-level taxonomy of the German *Mastodonsaurus* material, there is no basis for diagnosing *M. lavisi*, but neither can it be assumed to be indeterminable. It seems most practical to retain the name, albeit as a *nomen dubium*, as a convenient label for the Otter Sandstone mastodonsaurid material.

Referred material from the Otter Sandstone. As *Mastodonsaurus lavisi* is a *nomen dubium*, the following *Mastodonsaurus* material is referred to that species solely on the basis of locality and horizon: BMNH R.331, posterior region of right mandible collected by H. J. Carter from the type locality (Carter 1888); four boxes of fragments collected by Carter are registered as R.331, but the mastodonsaur mandible is the only significant specimen; referred to *M. lavisi* by Paton (1974); EXEMS 60/1985.287, left postfrontal and parietal (Text-fig. 2A), collected by P. S. Spencer; EXEMS 60/1985.309, left tabular and parts of squamosal and supratemporal (Text-fig. 2B, C), collected by P. S. Spencer, and referred to by Spencer and Isaac (1983) as a fragment of *Cyclotosaurus*.

Description of new material. EXEMS 60/1985.287 (Text-fig. 2A) comprises the attached left postfrontal and left parietal of a large temnospondyl. Scaling these bones against a skull of *Mastodonsaurus cappeleensis* figured by Wepfer (1923) suggests a midline skull length of 290 mm. The two bones bear coarse shallow sculpture with narrow ridge-systems. Some of the confluent sculpture pits on the orbital margin of the postfrontal may represent a lateral-line sulcus. The anterior end of the postfrontal is incomplete and it is impossible to ascertain whether it contacted the prefrontal or not. The postfrontal is relatively elongate and is almost as large as the parietal. The pineal foramen is situated about halfway along the parietals and hence well behind the posterior edge of the orbits.

The dermal sculpture resembles that of mastodonsaurids rather than capitosaurids and the large elongate postfrontal resembles that of the early mastodonsaurid *Mastodonsaurus cappeleensis* from the Anisian of Kappel near Villingen, Baden-Württemberg, West Germany. Using WARMS Gz.20, a larger skull fragment of the Warwickshire *Mastodonsaurus* material, Paton (1974, table 1) was able to show that it also corresponded to *M. cappeleensis* in orbit shape, size and position. In capitosaurids, the orbit length was 45–85% of the interorbital width, in WARMS Gz.20 and *M. cappeleensis* 120–125%, in the larger Ladinian *Mastodonsaurus* species over 200%. Unfortunately, no comparative study has been undertaken of the various *Mastodonsaurus* specimens from the Anisian, Ladinian and Carnian of Baden-Württemberg and we do not know whether proportional differences such as those described above are of systematic significance or simply related to absolute size.

EXEMS 60/1985.309 (Text-fig. 2B, C) comprises the left tabular and parts of the squamosal and supratemporal of a very large temnospondyl. Scaled against figures of *Mastodonsaurus* skulls, it appears to be derived from a skull of about 600 mm midline length. The suture between the tabular and the other bones is densely convoluted. The sculpture on the dorsal surface of the bones is coarse and shallow. The tabular is a curved, slightly elongate bone thinning out at its distal extremity and clearly does not suture with any other bone behind the otic notch. The curvature of the tabular is such that the distal end was laterally rather than postero-laterally directed. The deep open otic notch, partly bordered by a long curved tabular bearing coarse sculpture, is characteristic of large specimens of *Mastodonsaurus*, but not of any particular species. Some specimens of *M. giganteus* from Gaildorf (e.g. SMNS 4707 and 54679) are very similar and the specimen is closely comparable to WARMS Gz.9 from Warwickshire (Paton 1974, fig. 6) which Paton attributed to *M. lavisi*. The new undescribed *Mastodonsaurus* material from the Lettenkeuper of Kupferzell (Wild 1980b) includes skulls over a wide size range which demonstrate that the tabular is small in skulls of 300 mm length but elongates later in ontogeny (A.R.M. pers. obs.). A few capitosaurids have similar tabulars (e.g. *Parotosuchus nasutus* Welles and Cosgriff 1965, fig. 19 and *Parotosuchus megarhinus* Chernin 1974, fig. 8) but the dermal sculpture is finer, deeper and more reticulate.

Discussion. The Mastodonsauridae is at present a neglected family. The full range of German *Mastodonsaurus* material has not been subjected to comprehensive comparative study this century and meaningful comparisons are still difficult. Beyond the genus *Mastodonsaurus*, there is uncertainty as to what constitutes a primitive mastodonsaurid. Some capitosauroids may in fact be primitive mastodonsaurids with only one or two of the specializations of *Mastodonsaurus*. *Kestrosaurus dreyeri* Houghton, 1925 has generally been considered to be an aberrant capitosaurid, but Ochev (1966) placed it in the new family Bukobajidae which Shishkin (1980) later reduced in

synonymy with the Mastodonsauridae. '*Parotosaurus*' *lapparenti* Lehman, 1971 was also assigned to the Mastodonsauridae by Shishkin (1980). Both of these forms have double anterior palatal vacuities and laterally directed tabulars, and appear to be primitive mastodonsaurids with a gradistic resemblance to *Benthosuchus*.

The following observations can be made, however. Firstly, no mastodonsaurid-producing locality is known to have more than one species present. As the holotype of *M. lavisi* is a mandible from the Otter Sandstone, other mastodonsaur fragments from this formation can be placed under the name *M. lavisi* with confidence. Secondly, the proportions of the orbits and the circumorbital bones of specimens EXEMS 60/1985.287 from Devon and WARMS Gz.20 from Warwickshire both show the closest resemblance to the primitive *Mastodonsaurus cappelenensis* Wepfer, 1923 from the Upper Bunter of Kappel in Baden-Württemberg, West Germany. This does not demonstrate the unity of the British material from the two areas nor does it demonstrate synonymy with the German species. It suggests either that all three populations belong to a similar primitive evolutionary grade within the genus *Mastodonsaurus* or alternatively that all three populations are simply of similar-size specimens with similar orbital proportions. Because of the latter possibility, it is best to maintain the Warwickshire material as *Mastodonsaurus* sp. indet. (as no species name uniquely applies to it), the Devon material as *M. lavisi*, and the Kappel material as *M. cappelenensis*, but the three populations may represent from one to three species of mastodonsaurid. Consequently, stratigraphical conclusions based on such material should be treated with great circumspection.

Family BENTHOSUCHIDAE Efremov, 1940

Genus EOCYCLOTOSAURUS Ortlam, 1970

Type species. Eocyclotosaurus woschmidti Ortlam, 1970

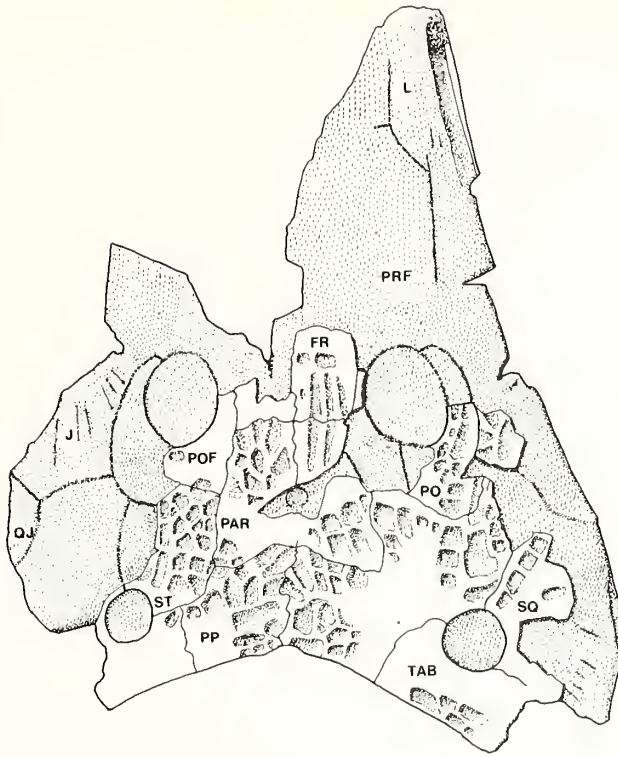
Eocyclotosaurus sp.

Text-figs 3 and 4.

Material. EXEMS 60/1985.72, damaged posterior skull roof with internal cast of left cheek (Text-fig. 3), from the Otter Sandstone below High Peak near Sidmouth, Devon and reported by Spencer and Isaac (1983) as a skull of *Cyclotosaurus*; EXEMS 60/1985.310, right tabular and parts of squamosal, supratemporal and postorbital (Text-fig. 4A); EXEMS 60/1985.75, an incomplete left clavicle (Text-fig. 4B), referred here with doubt; all collected by P. S. Spencer.

Description. EXEMS 60/1985.72 (Text-fig. 3), the most complete amphibian specimen yet collected from the Otter Sandstone Formation, is a partial skull of a small capitosauroid temnospondyl. Regions represented by bone include the skull table and parts of the interorbital area and cheeks; the rest of the cheeks and the right posterior region of the snout are represented by a weathered endocast, the part exposed at the time of collection. Most of the snout had already been weathered away prior to collection. The dermal bones of the right cheek, skull roof and interorbital region were all present *in situ* but were unfortunately damaged during excavation and have been reassembled. The palate is not exposed. The skull is estimated to have been 250 mm long, 150 mm wide from quadrate to quadrate, and 30 mm deep at the back, hence very low in profile. In most respects it is a typical capitosauroid skull and only key features need be discussed.

The dermal bones bear deep reticulate sculpture. There are no well-preserved lateral-line sulci although elongate pits on the supratemporals may represent poorly expressed sulci. The otic notch is completely closed by a stout extension of the tabular suturing with the squamosal. The length of this suture is about equal to the diameter of the otic notch. The posterior edge of the skull table is concave but appears to consist of two straight edges meeting medially at a distinct obtuse angle. The distal margin to the orbit is represented only by endocast on both sides, but on the left side the suture-lines are clearly visible. They show that the jugal was excluded from the orbit margin by an anterior extension of the postorbital extending forwards to the anterior margin of the orbit. Although the prefrontal shape is not determinable, it is probable that the postorbital sutured with the prefrontal ahead of the orbit; the postorbital has the same anterior extent as in German and French *Eocyclotosaurus* specimens in which suturing with the prefrontal occurs. Part of the corresponding suture is

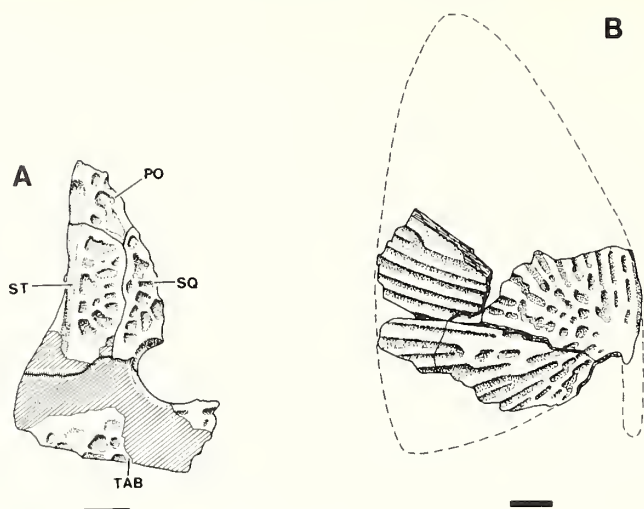


TEXT-FIG. 3. *Eocyclotosaurus* sp. EXEMS 60/1985.72, incomplete skull roof in dorsal view. Abbreviations: see Text-figure 2. Scale bar, 10 mm.

visible on the endocast on the right side as well (Text-fig. 3). The relationship between the prefrontal, the postfrontal and the frontal is unfortunately difficult to observe because of damage to the bones. On the right side, the pre- and postfrontals are represented only by damaged scraps of bone but the frontal appears to be inset with an exposed sutural edge along its distal margin. This indicates that the pre- and postfrontals probably met mesially to the orbit and excluded the frontal from the orbit margin. Although the snout is poorly preserved, it can be seen that the sides converge anteriorly, which implies a narrow anterior snout, rather than a broad parallel-sided snout.

Discussion. The specimen is clearly one of the capitosaurid or benthosuchid temnospondyls with a completely enclosed otic notch. In the Triassic of western Europe, the genera *Cyclotosaurus*, *Stenotosaurus*, and *Eocyclotosaurus* all have such notches. Their characteristics and relationships have recently been discussed by Kamphausen and Morales (1981), Kamphausen (1983) and Morales and Kamphausen (1984). The apparently narrowing snout and the anteriorly extending postorbital excluding the jugal from the orbit margin characterize the genera *Eocyclotosaurus* and *Stenotosaurus*. *Cyclotosaurus* species have the jugal entering the orbit margin and have broad snouts. The prefrontal-postfrontal contact identifies the specimen as *Eocyclotosaurus* rather than *Stenotosaurus* in which the frontal enters the orbit margin. These character-states suggest that the specimen is a skull of *Eocyclotosaurus* and all other visible features are consistent with this identity.

Kamphausen and Morales (1981) established the generic unity of the *Eocyclotosaurus* material from the Upper Bunter of France and West Germany but did not attempt to provide separate diagnoses for the two species *E. lehmani* (Heyler) and *E. woschmidtii* Ortlam. There are no obvious discriminating features between the species as described and the problem of whether this material



TEXT-FIG. 4. *Eocyclotosaurus* sp. A, EXEMS 60/1985.310, fragment of right skull table. B, EXEMS 60/1985.75, incomplete left clavicle. Abbreviations: see Text-figure 2. Scale bar, 10 mm.

represents one or two species is still being studied by Kamphausen. For this reason, the Otter Sandstone material is not assigned to a species but simply identified as *Eocyclotosaurus* sp.

Possible further referred material. The following two specimens are not in themselves diagnostic but are consistent with attribution to *Eocyclotosaurus* sp. and can be referred here with various degrees of confidence.

EXEMS 60/1985.310 (Text-fig. 4A) is a fragment of dermal skull roof from the region of the right otic notch. It is made up of an abraded right tabular and well-preserved parts of the right supratemporal, squamosal, and postorbital. The sculpture is relatively deep and reticulate. The supratemporal has broken along the lateral-line sulcus and only the distal part of the bone remains. The sulcus can be seen to be deep but its width cannot be determined. The otic notch is closed, the tabular running behind it as a stout structure, broadening distally towards the region where it would meet the squamosal. The specimen appears to be identical in all significant respects with the corresponding region in EXEMS 60/1985.72 and may also be referred to *Eocyclotosaurus* sp.

EXEMS 60/1985.75 (Text-fig. 4B) is an incomplete left clavicle of a capitosauroid temnospondyl. In shape, size, and texture of sculpture it is most consistent with attribution to the cranial material described above and is cautiously referred here.

Family CAPITOSAURIDAE Watson, 1919

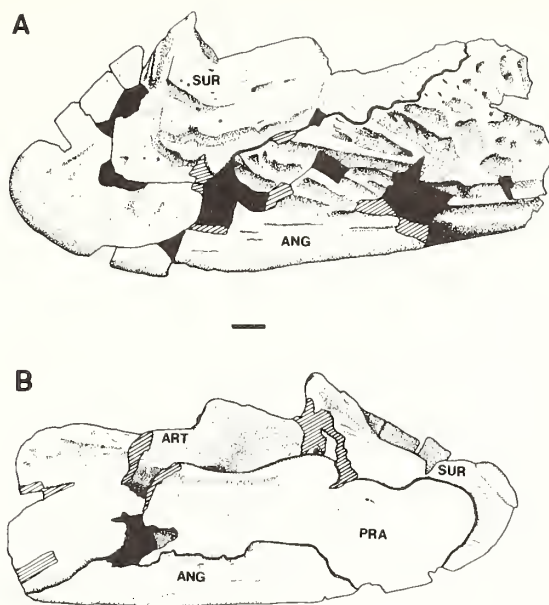
Capitosauridae incertae sedis

Text-fig. 5

Material. EXEMS 60/1985.78, posterior region of right mandible (Text-fig. 5A, B), collected by P. S. Spencer, and referred to by Spencer and Isaac (1983) as a mandible of *Cyclotosaurus*.

Description. This specimen comprises the greater part of the post-dentary region of a massive right mandible. The preserved elements are the surangular, prearticular, articular, and the posterior region of the angular. The angular bears deep coarse sculpture which extends slightly on to the surangular. A broad, shallow lateral-line sulcus, the mandibular sulcus, extends back from the ventrodistal side of the angular and curving dorsally behind it up to the dorsal side of the retroarticular process (Text-fig. 5A). Two branches extend forward along the external face of the surangular, the lower is the oral sulcus and the upper is the accessory sulcus (terminology as in Jupp and Warren 1986). Behind the mandibular sulcus, the external face of the retroarticular process has a few striations but does not have a sculptured surface. The ventral edge of the mandible is narrow

TEXT-FIG. 5. *Capitosauridae incertae sedis*. EXEMS 60/1985.78, posterior region of right mandible. A, buccal view. B, lingual view. Abbreviations: ANG, angular; ART, articular; PRA, prearticular; SUR, surangular. Scale bar, 10 mm.



and sharply concave. The retroarticular process is broadly rounded in lateral aspect, and is a slightly elongated triangle in dorsal view. The articular surface with the quadrate is saddle shaped. The foramen for the chorda tympani is present and set high on the side of the jaw.

Discussion. Comparison with the mandibular fragments described and tabulated by Paton (1974, table 2) shows complete correspondence to the Warwickshire specimens which she assigned to *Cyclotosaurus pachygnathus*. The nature of the sculpture and the lateral-line sulci, the high position of the chorda tympani foramen, the absence of sculpture on the retroarticular process and the shape of that process all serve to identify it as a capitosaurid or benthosuchid rather than a mastodonsaurid. It is clearly not attributable to *M. lavis*. The massive construction and the saddle-shaped articular surface correspond to those of a large *Cyclotosaurus* or *Parotosuchus* rather than a lightly built *Stenotosaurus* or a benthosuchid. It has all the characteristics of those Warwickshire mandibles such as GSM 27964 that Paton assigned to *Cyclotosaurus pachygnathus*. However, referring this specimen to *C. pachygnathus* is unsatisfactory because, by Paton's (1974, p. 280) own admission, *C. pachygnathus* is an undiagnosed aggregation of large cyclotosaur material from Warwickshire placed under one name for systematic stability and general convenience. Some of it certainly pertains to a *Stenotosaurus* or *Cyclotosaurus* of massive construction, but is of uncertain unity, cannot be comparatively diagnosed with the German material, and is effectively *Capitosauridae incertae sedis*, with the name *C. pachygnathus* a *nomen dubium* restricted to the lectotype specimen designated by Paton. However, much of the Warwick material is not demonstrably cyclotosaurian. In assuming the unity of this capitosaurid material, Paton did not attempt to compare any of it with open-notched *Parotosuchus* and *Eryosuchus*, both of which are present in Middle Triassic assemblages. A fragment of massive capitosaurid which does not include the otic notch is as likely to be *Parotosuchus* or *Eryosuchus* as *Cyclotosaurus*. Morales (1987) has noted that there is no certain *Cyclotosaurus* material from pre-Carnian beds and that '*Cyclotosaurus*' *randalli* Welles, 1947 from the Middle Triassic of the Moenkopi Formation is indeterminate but probably a benthosuchid. As the Otter Sandstone specimen is from a geographically distinct locality, and as unwarranted stratigraphical assumptions might be drawn if it and the Warwickshire material were assigned to the same genus or species, it is simply assigned to *Capitosauridae incertae sedis*.

Indeterminate temnospondyl fragments

Several other specimens from the Otter Sandstone clearly derive from temnospondyl amphibians but are not determinable. Six of these specimens which have numbers prefixed by EXEMS 60/1985, are as follows: .4, .79, .183, labyrinthodont teeth or palatal tusks; .96, .148, fragments of sculptured dermal bone, probably from skull roof; .308, half of a small interclavicle. A seventh specimen is EXEMS 7/1986.2, the posterior half of the right prefrontal of a benthosuchid or capitosaurid.

Class REPTILIA

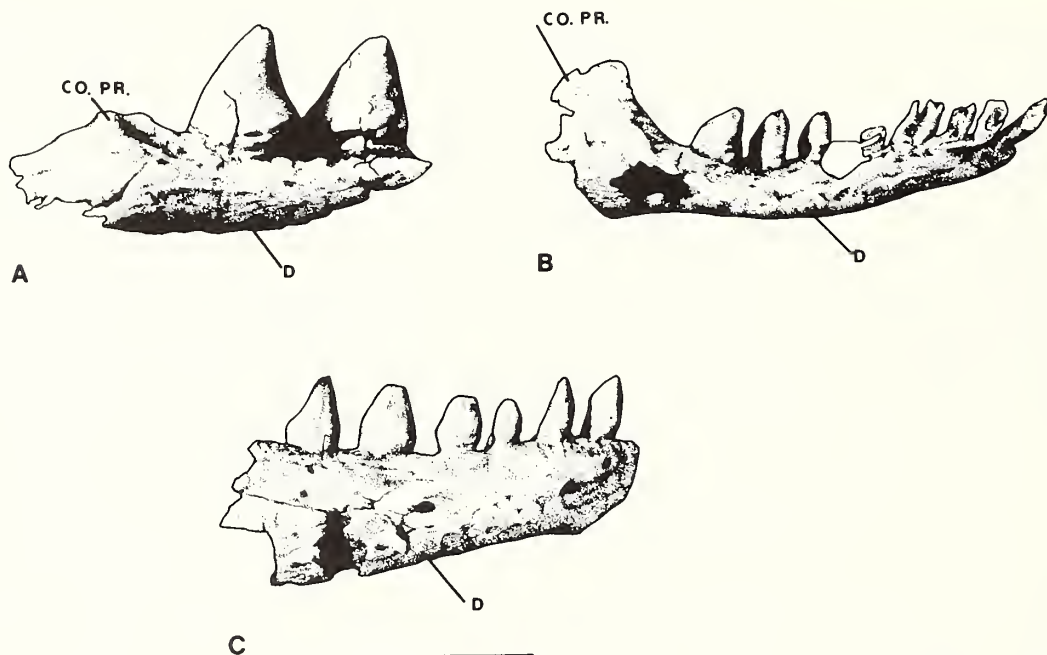
Order PROCOLOPHONIA

Family PROCOLOPHONIDAE Cope, 1889

Procolophonidae incertae sedis

Text-figs 6 and 7A, B

Material. EXEMS 60/1985.87, a right dentary fragment (Text-fig. 6A), referred to by Spencer and Isaac (1983) as a specimen of the procolophonid *Leptopleuron*; EXEMS 60/1985.154, a right dentary (Text-fig. 6B), reported as a sphenodontid by Spencer and Isaac (1983); EXEMS 60/1985.311, an incomplete right dentary (Text-fig. 6C), EXEMS 60/1985.3, a fragmentary left maxillary (Text-fig. 7A), reported by Spencer and Isaac (1983) as a sphenodontid; EXEMS 60/1985.9, an incomplete interclavicle (Text-fig. 7B), correctly identified by Spencer and Isaac (1983). All specimens were collected by P. S. Spencer.



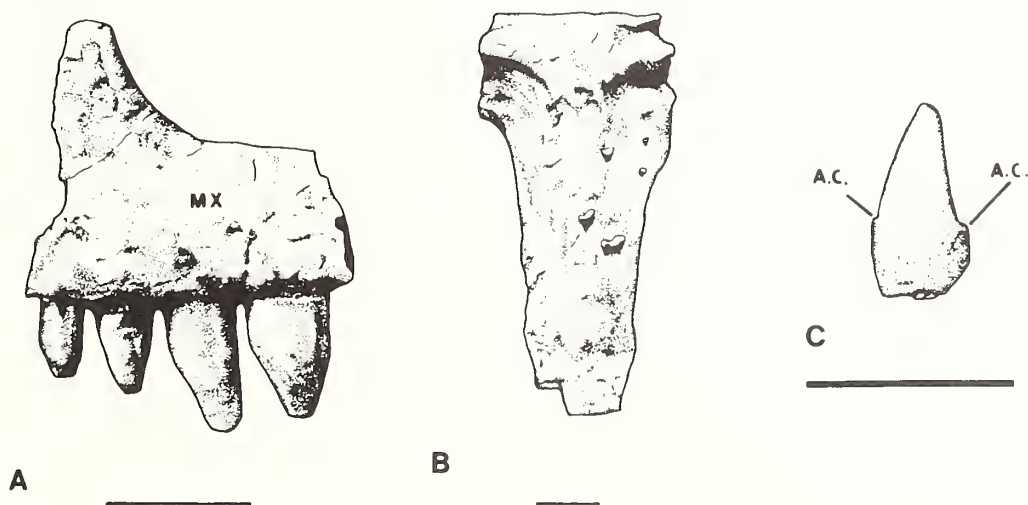
TEXT-FIG. 6. *Procolophonidae incertae sedis*. A, EXEMS 60/1985.87, fragment of right dentary. B, EXEMS 60/1985.154, juvenile right dentary. C, EXEMS 60/1985.311, juvenile right dentary. All in lateral view. Abbreviations: CO. PR., coronoid process; D, dentary. Scale bar, 5 mm.

Description. EXEMS 60/1985.87 was the only jaw specimen correctly identified by Spencer and Isaac (1983) as procolophonid, but whether it can be attributed to *Leptopleuron*, as they suggest, is questionable. The dentary, which is predominantly exposed in lateral aspect (Text-fig. 6A), is 9.0 mm long and, in addition to the

two posteriormost teeth, it retains the broken base of a coronoid process. Superficially at least, the broadly-based obtusely conical teeth display an acrodont attachment. The posterior tooth is 2.7 mm high and that in front of it is 2.4 mm high. Their bulbous appearance in lateral aspect is typically procolophonid. The teeth of this specimen (the only one in which they are completely exposed from the matrix) are not transversely broadened. However the maximum development of transverse broadening in procolophonids is seen most frequently in the teeth immediately anterior to these positions.

Two further dentary fragments are more complete, but somewhat smaller than EXEMS 60/1985.87, and they are regarded here as juveniles. EXEMS 60/1985.154 is 12 mm long and retains nine teeth and a pronounced coronoid process (Text-fig. 6B). The element is complete anteriorly, with the mandibular symphysis partly embedded in matrix. Spencer and Isaac (1983, p. 268) referred to this specimen as a sphenodontid, but it lacks typical sphenodontid dental characters such as tooth flanges, distinct successional hatchling and additional tooth series, and at least partial alternation in tooth size (Fraser 1986a; Whiteside 1986), nor is there a marked posteriorward increase in tooth height, nor any indication of extensive lateral wear facets correlated with the shearing jaw action so typical of sphenodontids (Robinson 1973; Gorniak *et al.* 1982; Fraser and Walkden 1983). Where exposed, wear facets appear to be confined to the apical surfaces of each tooth. The prominent incisiform anterior teeth are inclined anteriorly and somewhat laterally, a characteristic readily observed in *Procolophon* and *Orenburgia*.

EXEMS 60/1985.311 (Text-fig. 6C) is a third dentary fragment, also exposed from the right side. It is incomplete posteriorly and lacks the coronoid process, but the six exposed teeth are rather better preserved than in the previously described specimens. In all specimens, tooth attachment appears to be acrodont. The first two teeth are equal in height to the more posterior members of the tooth row, yet they are markedly narrower and thus incisiform in appearance. By contrast, the posterior three teeth are broader based, and in lateral aspect they are widest at a point approximately mid-way up the crown. The resulting profile has been described as barrel-shaped by Malan (1963) and characterizes most procolophonids (e.g. *Procolophon*, *Thelegnathus*, *Tichvinskia*).



TEXT-FIG. 7. A and B, *Procolophonidae incertae sedis*; A, EXEMS 60/1985.3, left maxillary in lateral view; B, EXEMS 60/1985.9, interclavicle in ventral view. C, ?*Tanystropheus* sp., EXEMS 60/1985.143, an isolated tooth. Abbreviations: A.C., accessory cusps; MX, maxillary. Scale bar, 2 mm.

EXEMS 60/1985.3 is a maxillary fragment bearing four teeth (Text-fig. 7A) which Spencer and Isaac (1983) referred to as a sphenodontid. They believed it to represent a right element in association with a partly preserved jugal. Presumably they took a faint line running across the specimen as the suture between the two bones. However the dental morphology is consistent with that of a procolophonid and, other than the acrodont implantation, the dentition shows no sphenodontid characteristics. The enlarged orbit of procolophonids is characterized by the great expansion of the posterodorsal corner so that the ventral margin, normally formed by the jugal and (to a variable extent) the maxillary, gently slopes posterodorsally. The preserved orbital

margin of EXEMS 60/1985.3 is too abrupt for it to be anything but the anterior margin. Furthermore the slight recurvature of the teeth supports the interpretation of this fragment as part of a left-sided element. Consequently, if the line referred to above is a suture, then it is between the lacrimal and maxillary rather than the jugal and maxillary. However the line is poorly defined and it seems more plausible to attribute it to post-mortem damage.

EXEMS 60/1985.9 is an incomplete T-shaped interclavicle (Text-fig. 7B) which is characteristically procolophonid. Although the interclavicles of sphenodontids are also T-shaped, they are usually much more slender and they lack the broad median bar that is so prominent in EXEMS 60/1985.9.

Discussion. There is nothing to suggest that more than one procolophonid species is represented in the Otter Sandstone, and the variation in size can be satisfactorily explained as ontogenetic. The only characteristics which may be of systematic or stratigraphical value are those of the mandibular dentition, which may be summarized as follows: the mandible possesses nine acrodont teeth (a primitively high number within the Procolophonidae), the anterior incisiform teeth are inclined anterolaterally, and the posterior molariform teeth are barrel-shaped (procolophonid characters) but appear to lack the derived conditions of being cuspidate or transversely broadened. The Otter Sandstone material thus appears to belong to a primitive procolophonid and its closest resemblance is to the Middle Triassic (Anisian) *Anisodontosaurus greeri* from the Holbrook Member of the Moenkopi Formation of Northern Arizona. Although *Anisodontosaurus* was recorded by Welles (1947) as *Reptilia incertae sedis*, and by Murry (1987) as a primitive sphenodontid, it appears to be a primitive procolophonid. The dentary bears twelve teeth differentiated into incisiforms and broad-based molariforms. Welles (1947) described the two posteriormost teeth of *Anisodontosaurus* as acrodont in implantation, but noted that the more anterior teeth project further down into the dentary and approach a thecodont condition. However, it is sometimes impossible clearly to distinguish between different forms of tooth implantation (Fraser and Shelton 1988). Although procolophonids are normally considered to be acrodont, the teeth in some specimens appear to be positioned in shallow sockets (Fraser 1986b), not unlike the tooth implantation described in *Anisodontosaurus*. Although the former possesses rather more teeth, *Anisodontosaurus* and the Otter Sandstone procolophonid are primitively more similar to each other than to any other procolophonid.

Typical early Triassic procolophonids such as *Procolophon*, *Koiloskiosaurus*, *Sclerosaurus*, *Eumetabolodon*, and *Thelegnathus* are more derived than the Otter Sandstone form in that they have transversely broadened 'molariform' teeth, and a rudimentary bicuspidate condition is sometimes present. The dentitions of *Koiloskiosaurus* and *Sclerosaurus* from the Upper Buntsandstein of Germany are incomplete but, although they appear to possess between seven and nine teeth in each jaw ramus, at least some of these are transversely broadened (Huene 1911, 1943). In late Triassic forms, the bulbous profile is accentuated and the molariform teeth are invariably transversely broadened and either bicuspidate (*Leptopleuron*) or tricuspidate (forms in the English fissure sediments (Fraser 1986b)).

Some early and most late Triassic procolophonids show a marked trend towards reduction in overall tooth numbers. The third Buntsandstein genus, *Anomoiodon* (Huene 1939), is small with a skull length just over 30 mm and hence close in size to the Otter Sandstone material. *Anomoiodon* resembles the Otter Sandstone material in that all the marginal teeth are conical and no transverse broadening is apparent. On the other hand, despite the incomplete preservation, there would appear to have been no more than five teeth in the mandible in contrast to nine in EXEMS 60/1985.54. Thus there is no clear basis for assigning the Devon specimens to any one of the contemporaneous German genera. The Otter Sandstone procolophonid material is too fragmentary to be determinable below family level, but it does appear to belong to a very primitive number of the family.

Division ARCHOSAUIROMORPHA
Order PROLACERTIFORMES
Family TANYSTROPHEIDAE Romer, 1945
Genus TANYSTROPHEUS Meyer, 1852

cf. *Tanystropheus* sp.

Text-fig. 7c.

Material. EXEMS 60/1985.143, a tricuspid tooth (Text-fig. 7c), collected by P. S. Spencer, and reported as a therapsid tooth by Spencer and Isaac (1983).

Description. A single tricuspid tooth, approximately 1.0 mm high, bearing two small accessory cuspules on either side of the main cusp. There is some resemblance to the large teeth of the Norian pterosaur *Eudimorphodon* (Wild 1978), but the latter are considerably larger and more elongate. A better comparison is with the teeth of the prolacertiform *Tanystropheus* (Wild 1973, 1980a). Wild (1980a, fig. 4) figures several teeth from a *Tanystropheus* skull including the fourth dentary tooth (fig. 4c) which is almost identical to 60/1985.143 in overall shape and relative size of cusp and cuspules.

Class AMNIOTA *incertae sedis*

Material. EXEMS 60/1985.88, an elongate bone collected by P. S. Spencer. Referred to by Spencer and Isaac (1983, p. 269) as a neural spine of 'the pelycosaur *Ctenosaurus*'.

Description. This specimen is a long straight bone, 514.9 mm in length according to Spencer and Isaac, but broken at both ends. It has a slightly flattened figure-of-eight cross-section and a surface pattern of fine ridges and foramina. It seems to be part of the axial skeleton of a large reptile, but beyond this general identification, it has proved difficult to place anatomically or systematically. As well as two of the authors (A.R.M. and M.A.T.), several colleagues, including Drs M. J. Benton, A. R. I. Cruickshank, G. M. King, and D. B. Norman have examined the specimen. There is no basis for attributing it to the pelycosaurs, and in fact the Triassic '*Ctenosaurus*' material, now renamed *Ctenosauriscus*, has been shown by Krebs (1969) to be one of a series of long-spined Middle Triassic thecodontian-grade archosaurs. In the specimen from the late Middle Buntsandstein figured by Krebs (1969, pl. 1), the tallest neural spine is a long straight flattened bone about 640 mm long. The Otter Sandstone specimen could be a long neural spine of such a ctenosauriscid or a rib of a large dicynodont therapsid such as a kannemeyeriid. Its size is compatible with either identity but it appears to be somewhat narrow in relation to its length for either interpretation. There is slight asymmetric curvature at one end which seems to be too great for a ctenosauriscid spine and too little for a dicynodont rib. The identity of this specimen is left open.

STRATIGRAPHY

Recent history

As noted in the introduction, the only available evidence for dating the Otter Sandstone is the vertebrate fossil fauna itself. Previously, only the few fragments of rhynchosaur and temnospondyl collected in the nineteenth century have been considered for the purposes of dating. Walker (1969) noted the Sidmouth rhynchosaur as 'a more primitive species' of *Rhynchosaurus* than those known from the Midlands and Shropshire. The Midlands *Rhynchosaurus* derives from the Bromsgrove Sandstone Formation of the Sherwood Sandstone Group, while the Shropshire material derives from the Helsby Sandstone Formation of the Sherwood Sandstone Group and the Tarporley Siltstone Formation of the Mercia Mudstone Group (Warrington *et al.* 1980). However, no precise independent dating of the Midlands or Shropshire reptiles had then been achieved and Walker could only suggest an age within the range of late Anisian to earliest Carnian, probably early-mid Ladinian. Unfortunately, Walker (1969) did not explicitly state whether this dating also applied to the Otter Sandstone material. As a result, Laming (1982) cited Walker as ascribing an early-mid Ladinian age to the Devon rhynchosaur, whereas Warrington *et al.* (1980) and Spencer and Isaac (1983) took Walker's statement that the Devon rhynchosaur was more primitive to imply an Anisian date for the Otter Sandstone Formation. Walker later (1970) said of the Shropshire and Midlands animals that 'a late Anisian, or, preferably, a Ladinian age seems to be implied'. He also repeated his opinion that the Devon material was more primitive and tentatively suggested that the

Otter Sandstone Formation was older than the Shropshire and Midlands horizons, and so presumably an Anisian age was implied. Most subsequent assignments of an Anisian date to the Otter Sandstone Formation can be traced back to Walker's observation (see Benton 1990 for a discussion). The English *Rhynchosaurus* material, including several new specimens from the Otter Sandstone, has recently been restudied by Benton (1987, 1990). The Otter Sandstone *Rhynchosaurus* represents a distinct species from the Midlands material but the characters of the various species do not suggest any obvious stratigraphical sequence of the British Triassic sites (Benton 1990).

Paton (1974) reviewed the temnospondyl amphibians of the English Triassic and suggested that the Otter Sandstone vertebrates were coeval with the Shropshire and Midlands animals. She associated Devon and Midlands *Mastodonsaurus* material in the single species *M. lavisi* which implied that the two horizons were contemporaneous. Paton compared the mastodonsaur and the two cyclotosaur species from the English Triassic with German material and argued that *M. lavisi* and *Cyclotosaurus leptognathus* indicated a Scythian/Anisian age, while *Cyclotosaurus pachygnathus* indicated a Carnian/Norian age. She appears to have taken an average of the two ages, ascribing the Midlands and Devon amphibians to the early Ladinian, after taking Walker's (1969, 1970) reptile evidence into account. Thus the previously published situation for the age of the Otter Sandstone Formation vertebrates is that it is either Anisian (based on Walker's suggestion that the rhynchosaur is more primitive than the presumed Ladinian Midlands material) or Ladinian (based on Paton's conclusion that the material is contemporaneous and that two of the amphibians suggest an Anisian age and one suggests a Carnian age).

New evidence

Attempts to date the British Triassic vertebrate-bearing assemblages by comparison with the French and German sequences are handicapped by the presence of the Muschelkalk through much of the Anisian and Ladinian in mainland Europe. Consequently, comparisons of continental vertebrates must either be with the Upper Buntsandstein/Röt/*Voltzia* Sandstone faunas of uppermost Scythian/basal Anisian age, or with the Lettenkohle faunas of latest Ladinian age. Middle Anisian-Middle Ladinian continental faunas are barely represented in the Muschelkalk, and there are no sequential series of stratigraphically restricted taxa, and so only relatively crude comparisons and correlations are possible. Of the new material reported in this work, the capitosaurid jaw is least useful, merely supporting a Triassic age for the Otter Sandstone. All other forms can be used to narrow the possibilities to give a more precise assessment.

The genus *Dipteronotus* is known from the Scythian of Europe to the Carnian/Norian of Morocco but the Otter Sandstone species *D. cyphus* is otherwise known only from the fish assemblage from the Building Stones, the upper member of the Bromsgrove Sandstone Formation at Bromsgrove. Warrington (1967, 1970) dated the entire Bromsgrove Sandstone in a borehole at Bromsgrove as Scythian to early Ladinian using acritarch and miospore evidence, and this would imply an Anisian – early Ladinian age for *D. cyphus*. Comparisons of Bromsgrove vertebrates with material from Germany suggest a date at the later end of this range, particularly the presence of the shark *Palaeobates keuperinus* (*Acrodus* sp. of Wills 1907, 1910) and the palaeoniscoid *Gyrolepis albertii* (see Appendix for further details). *Palaeobates keuperinus* (Murchison and Strickland) occurs at several localities in the Bromsgrove Sandstone Formation and the Mercia Mudstone Group (it may be noted that the material of *Phoebodus brodei* Woodward from Shrewley consists of symphysial teeth of *Palaeobates keuperinus*). *P. keuperinus* resembles closely *P. angustissimus* (Agassiz) from the Upper Muschelkalk and Lettenkohle of Germany, Poland, and France. *G. albertii* is not only found in the Bromsgrove Sandstone Formation and Mercia Mudstone Group of the Midlands, but also continues into the Rhaetic. This species also occurs in Baden-Württemberg, Bavaria, and Thuringia where it is almost entirely confined to the Upper Muschelkalk. Thus *Dipteronotus cyphus* at Bromsgrove is in a horizon of Anisian to early Ladinian age and is associated with some fish found in the Ladinian upwards elsewhere. A late Anisian – early Ladinian age might be inferred for the Otter Sandstone on the basis of the presence of *D. cyphus*.

The genus *Eocyclotosaurus* has the most restricted stratigraphical range of any form described

here. *Eocyclotossaurus* species have been described from two European formations, *E. lehmani* from the *Voltzia* Sandstone of the Vosges in France and *E. woschnidti* from the Lower Röt of the Schwarzwald in West Germany. Both formations are equated with the Upper Bunter and are either late Spathian or early Anisian (uppermost Lower or lower Middle Triassic) in age (Morales 1987). There is also an undescribed *eocyclotossaur*, which is being studied by S. P. Welles and M. Morales (Morales 1987), from the Holbrook Member of the Moenkopi Formation of Arizona, which is believed to be early Anisian in age (Welles and Estes 1969; Morales 1987). The presence of this genus very positively suggests an Anisian age for the Otter Sandstone.

Mastodonsaurus species have been described from the Upper Bunter (Anisian) of Kappel in West Germany (*M. cappelenensis*) to the Schilfsandstein (Carnian) of Feuerbacher Heide, Stuttgart (*M. keuperinus*). As discussed above, the British material from both Devon and Warwickshire has some resemblance in interorbital proportions to the Anisian *M. cappelenensis* within the genus. However, in the absence of detailed comparisons among the Anisian, Ladinian, and Carnian *Mastodonsaurus* material from Germany, not much weight can be given to this observation and the material merely indicates an Anisian-Carnian date.

The procolophonid, though not precisely determinable, is clearly primitive in the number and narrowness of the mandibular teeth, and forms with such primitive features are found only in Scythian and Anisian horizons. Other reptiles clearly indicate a Middle Triassic age. The comparison of the isolated tricuspid tooth with the dentition of *Tanystropheus* supports a Middle Triassic assignment, *Tanystropheus* being known from the Anisian and the Ladinian of central Europe (Wild 1980a). If the elongate element proves to be a ctenosauriscid neural spine, this also supports a Middle Triassic age. Known ctenosauriscids are *Ctenosauriscus* from the Anisian Upper Buntsandstein of Germany (Krebs 1969), *Hypselorhachis* from the Ladinian Manda Formation of Tanzania, and *Lotosaurus* from the Middle Triassic of China.

A consideration of the Otter Sandstone assemblage as an association supports an Anisian age. The association of *Dipteronotus cyphus* (Anisian-basal Ladinian), *Eocyclotossaurus* (late Scythian-Anisian), *Mastodonsaurus* (Anisian-Carnian), primitive procolophonid (Scythian-Anisian), ?ctenosauriscid (Anisian-Ladinian) and ?tanystropheid (Anisian-Ladinian) has the Anisian as the only shared date. The fauna is in fact reminiscent of the Scythian/Anisian late Buntsandstein and *Voltzia* Sandstone faunas of Germany and France (Jörg 1969; Krebs 1969; Ortlam 1970; Gall *et al.* 1974; Kamphausen and Morales 1981), although *Rhynchosaurus* is conspicuously absent from the latter assemblages. The resemblance suggests that the Otter Sandstone fauna is an extension of the Anisian Upper Buntsandstein fauna.

THE OTTER SANDSTONE FAUNA

The Otter Sandstone appears to have been laid down on a flood-plain covered with small ephemeral braided streams and lakes (Laming 1982). The climate was semi-arid with long dry periods punctuated by seasonal rains and flash-floods. The vertebrate material is fragmentary, clearly transported and current-sorted, which can be inferred from the composition of the assemblage; teeth, tooth-bearing elements, and dense pieces of skull and pectoral girdle. The notable exception is the *Dipteronotus* material which is found as intact specimens in a laminated mudstone. Because of the derived nature of the assemblage, it bears an uncertain relationship to the original fauna (or faunas) and only a few observations can be made.

There seems to be distinct aquatic and terrestrial components to the fauna. The three types of temnospondyl amphibian were all superficially crocodile-like forms and all belong to families which are believed to have been fundamentally aquatic. The presence of three types of aquatic carnivore, some growing to at least 2 metres in length, suggests a rich fish fauna of which we currently have only one genus. It also suggests that there must have been at least some permanent water bodies among the aquatic environments on the flood-plain which gave rise to the Otter Sandstone.

The only frequent elements in the terrestrial fauna are the rhynchosaur *Rhynchosaurus*, a medium-sized herbivore, and the procolophonid, a small herbivore. Both appear to have been

adapted for feeding on particularly durable vegetation. The long bone appears to have represented a rarer medium-large herbivore, whether it belonged to a ctenosauriscid or a dicynodont. Notwithstanding earlier reports, there are no sphenodontids or insectivorous/carnivorous therapsids in the collected material. Spencer and Isaac (1983, p. 269) noted teeth and a skull fragment of an *Ornithosuchus*-like medium-sized carnivore. At present, the terrestrial component of the Otter Sandstone fauna does not appear to be diverse and perhaps consists of representatives of a few abundant specialists living in a semi-arid flood-plain environment.

Acknowledgements. We particularly thank Mr Patrick S. Spencer for generously donating his collection to the Royal Albert Memorial Museum, Exeter and thus making it available for this work. We are also grateful to Mr Kelvin I. Boot (Royal Albert Memorial Museum), Dr Rupert Wild and Dr Ronald Boettcher (Staatliches Museum für Naturkunde in Stuttgart) and Dr Angela C. Milner (British Museum (Natural History)) for permission to study material in their care. We further thank Dr M. J. Benton and Dr G. Warrington for improving the manuscript and for providing information on Triassic stratigraphy, Dr Michael J. Benton, Dr Arthur R. I. Cruickshank, Dr Gillian M. King and Dr David B. Norman for examining the long axial bone and permitting use to cite their opinions on its identity and Mr David J. Ward and Mrs Sandra E. Sequeira for photographic assistance.

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Typescript received 5 July 1989

Revised typescript received 3 November 1989

APPENDIX

Check-list of the pre-Penarth Group Triassic fishes of the British Isles (all material examined by B.G.G.).
MMG = Mercia Mudstone Group, SSG = Sherwood Sandstone Group.

Palaeobates keuperinus (Murchison and Strickland, 1840)

Bromsgrove Sandstone Formation (SSG) of Bromsgrove. Arden Sandstone Member (MMG) of Callow Hill; Mousley End; Shrewley; Knowle; Rowington; Shelfield Square, WARWICKSHIRE; and Burghill; Ripple; Pendock, HEREFORD and WORCESTER. Dane Hills Sandstone Member (MMG) of Shoulder of Mutton Hill; Dane Hills; New Parks; Aylestone Road, LEICESTERSHIRE.

Gyrolepis albertii Agassiz, 1835

Bromsgrove Sandstone Formation (SSG) of Bromsgrove, HEREFORD and WORCESTER (WARMS material). Colwick Formation (MMG) of Colwick Wood, NOTTINGHAMSHIRE. Arden Sandstone Member (MMG) Leamington, WARWICKSHIRE (Owen 1842 pl. 46, fig. 15; see Walker 1969). Dane Hills Sandstone Member (MMG) of Aylestone Road (*G. quenstedtii* of Browne 1893) and Spinney Hills (BMNH P.41626-9), LEICESTERSHIRE.

Dictyopyge catoptera (Agassiz, 1835)

Sherwood Sandstone Group of Dungannon, CO. TYRONE.

Dictyopyge superstes (Egerton, 1858)

Arden Sandstone Member (MMG) of Rowington, WARWICKSHIRE. This record is based on a partial body and is probably part of a dictyopygid as Woodward (*in* Swinnerton 1925) surmized. It shows no resemblances to *Woodthorpea* despite Swinnerton's (1925, p. 97) comments, and closely resembles *Dictyopyge socialis* (Berger) from the Upper Keuper of Colburg.

Dictyopyge sp. nov.

Colwick Formation (MMG) of Colwick Wood, NOTTINGHAMSHIRE. Known from a single specimen (BMNH P.5288), this novel dictyopygid has scales with posterior margins bearing three prominent projections.

?*Perleidus*

Wildmoor Sandstone Formation (SSG), Aggborough, HEREFORD and WORCESTER. This record (White 1950) is based on a single specimen which lacks head and tail, but nevertheless closely resembles *Perleidus*.

Dipteronotus cyphus Egerton, 1854

Bromsgrove Sandstone Formation (SSG) of Bromsgrove, HEREFORD and WORCESTER and Otter Sandstone of Sidmouth, DEVON.

'Semionotus' brodiei Newton, 1887

Arden Sandstone Member (MMG) of Shrewley, WARWICKSHIRE. This species is represented by five syntypes (BMNH P.7615), which bear no resemblance to the genus *Semionotus* (McCune 1986, p. 229). It is a small species with large dorsal ridge scales and deep flank scales. The tail is heterocercal, the suspensorium more or less upright and supraorbitals seem to be present. It appears to be a catopterid or a redfieldiid.

Semionotus metcalfei Swinnerton, 1928

Colwick Formation (MMG) of Woodthorpe and Colwick Wood (BMNH P. 9818), NOTTINGHAMSHIRE. Dane Hills Sandstone Member (MMG) of Spinney Hills, LEICESTERSHIRE ('semionotid fish' of Horwood 1907). This species is probably synonymous with *S. kapffi* Fraas, 1861 (McCune 1986, p. 230). It has ridge scales with spines and a single large suborbital.

Woodthorpea wilsoni Swinnerton, 1925

Colwick Formation (MMG) of Woodthorpe, NOTTINGHAMSHIRE. This is a small semionotid, apparently with a single suborbital.

Ceratodus laevisimus Miall, 1878

Bromsgrove Sandstone Formation (SSG) of Coten End, WARWICKSHIRE (*Ceratodus* cf. *C. kurii* of Wills 1910) and Bromsgrove, HEREFORD and WORCESTER. Mercia Mudstone Group of Ripple, HEREFORD and WORCESTER.

A TINY MICROSAUR FROM THE LOWER PERMIAN OF TEXAS: SIZE CONSTRAINTS IN PALAEOZOIC TETRAPODS

by ROBERT L. CARROLL

ABSTRACT. *Quasicaecilia texana* gen. et sp. nov., from the Lower Permian of Texas, is a very small microsauro in which the nasal bones form the front margin of the skull and the cultriform process of the parasphenoid is not in contact with the sphenethmoid. The bones of the otic-occipital region are fused to one another, and the otic capsule and stapes are very large relative to other cranial dimensions, giving a superficial resemblance to modern caecilians. Many of the unusual cranial features of this species may be attributed to its small size. The relatively large size of the sensory capsules in Palaeozoic amphibians with an adult skull length less than about 2 cm results in significant modification of the area of the otic capsule and jaw articulation.

PALAEOZOIC amphibians have customarily been divided into two large groups, the labyrinthodonts and the lepospondyls (Romer 1966; Carroll 1977, 1987). Labyrinthodonts are typified by a suite of primitive characters inherited from their ancestors among the rhinidistian fish.

- a. Squamosal embayment of cheek occupying position of rhinidistian operculum.
- b. Marginal teeth exhibiting labyrinthine enfolding.
- c. Large palatal fangs and associated replacement pits.
- d. Occipital condyle (where present) narrow and circular.
- e. Multipartite atlas-axis complex.
- f. Vertebral centra primitively consisting of crescentic ventral intercentrum and paired pleurocentra.

Lepospondyls are characterized by a suite of more derived characteristics.

- a. Absence of squamosal embayment.
- b. Lack of labyrinthine enfolding of marginal teeth.
- c. Absence of large palatal fangs and adjacent replacement pits.

Most lepospondyls have a wide or double occipital condyle and a single cylindrical centrum per segment.

Labyrinthodonts are certainly a paraphyletic group, including the ancestors of all more-derived tetrapods. Several recent attempts have been made to establish the affinities of the many groups termed lepospondyls, but as yet no consensus has been reached as to their specific relationships to the labyrinthodont groups, or to one another (Thomson and Bossy 1970; Gaffney 1979; Gardiner 1983; A. R. Milner *et al.* 1986; Gauthier *et al.* 1988; Panchen and Smithson 1988). In the absence of generally accepted relationships, it remains convenient to retain the descriptive terms labyrinthodont and lepospondyl.

In addition to similar derived features by which all lepospondyls are distinguished from labyrinthodonts, each individual group – aistopods, nectrideans, adelogyrinids, lysorophids and microsaurs – is distinguished from the others by numerous unique derived features. Lepospondyls also show a much higher degree of variability within each order than that exhibited by the labyrinthodonts in the pattern of the dermal bones of the skull, the configuration of the braincase, the length of the vertebral column, and the proportions and structure of the limbs. Labyrinthodonts

had a basically similar skeletal pattern from their first appearance in the fossil record in the Upper Devonian to their last appearance in the Cretaceous.

Shared derived features of the skeleton demonstrate that all tetrapods share a common ancestry above the level of the rhipidistian fish (Panchen and Smithson 1987). This implies that lepospondyls must have evolved from tetrapods having an anatomical pattern similar to that of known labyrinthodonts; however, no intermediates are recognized. This situation suggests that some complex of evolutionary constraints acted to retain a stereotyped anatomical pattern among the labyrinthodonts. The emergence of the various lepospondyl groups may be attributed to circumvention of these constraints.

In addition to the anatomical differences already mentioned, all lepospondyls are further distinguished from primitive labyrinthodonts by their smaller adult size. Some labyrinthodonts are as small as large lepospondyls, indicating that small size is not a *sufficient* factor in itself to result in the evolution of lepospondyl characters, but it seems a *necessary* factor, since none of the lepospondyls is the size of large labyrinthodonts. The larger Permian lepospondyls are highly derived members of this assemblage; all the early lepospondyls are much smaller.

Small size is an important attribute of the origin of many vertebrate groups: the modern amphibian orders (Carroll and Holmes 1980; Milner 1988), amniotes (Carroll 1970), and some lizard families (Rieppel 1988). Hanken (1983, 1989) has stressed its importance in the radical reorganization of the limbs and skulls of tiny living salamanders. The peculiar anatomy of the animal described in this paper provides a basis for considering the importance of skull size in influencing the cranial anatomy of Palaeozoic amphibians.

MATERIALS AND METHODS

This paper deals primarily with a single specimen (Text-fig. 1) collected by C. H. Sternberg in 1917 from the classic Texas Permian redbeds. The specimen had long been identified as *Cardiocephalus*, a gymnarthrid microsauro. The short antorbital region may have been attributed to breakage, and the great width of the parietals may not have been recognized due to the presence of longitudinal cracks that might have been identified as sutures separating relatively narrow parietals from more lateral tabular bones.

As preserved, the skull is approximately 14.5 mm long, and equally as wide. The anterior extremity is formed by the broad, short nasal bones. They show no area for attachment of the premaxillae, and those bones are otherwise missing. The posterior surface of each occipital condyle is broken off, precluding exact determination of the length of the skull. Most of the bones of the palate are missing or displaced, exposing the braincase ventrally.

The skull roof and occiput were largely exposed as a result of natural weathering of the matrix. The parasphenoid was also initially exposed. The remaining areas of the palate and braincase were prepared with a fine needle. The matrix is a hard, fairly homogeneous limey clay. It varies in colour from white to pink and in places was very difficult to differentiate from the bone.

SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA Linnaeus, 1758

Order MICROSAURIA Dawson, 1863

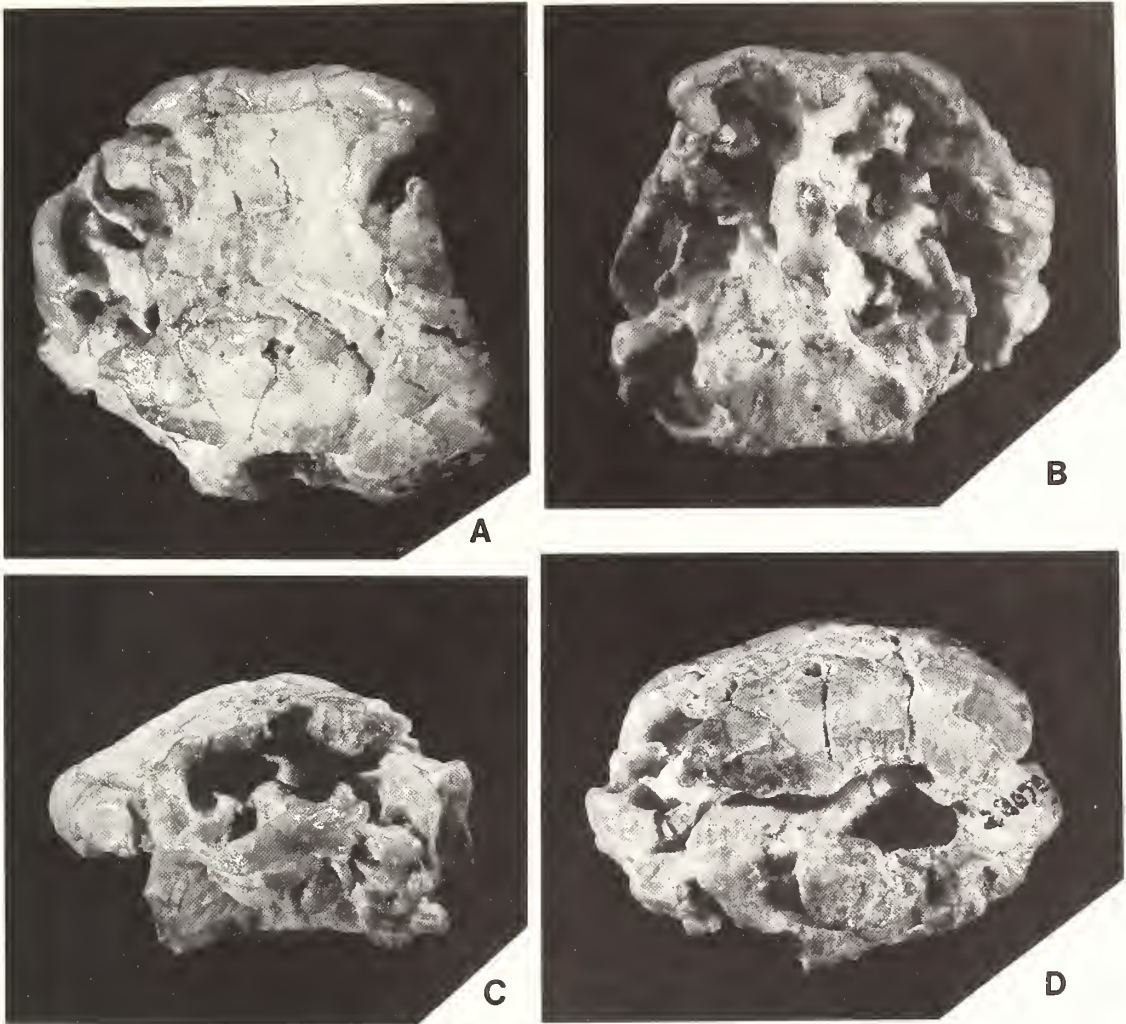
Suborder MICROBRACHOMORPHA Carroll and Gaskill, 1978

?Family BRACHYTELECHIDAE Carroll and Gaskill, 1978

Genus QUASICAECILIA gen. nov.

Type species. Quasicaecilia texana sp. nov.

Derivation of generic name. The generic name refers to several similarities with modern caecilians that are almost certainly not indicative of close relationship.



TEXT-FIG. 1. *Quasicaecilia texana*, type, United States National Museum, 22079. A, dorsal view of skull. B, obliquely anterior view of palate and braincase; postorbital bone that appears in drawings was removed prior to photographing. C, left lateral view of skull. D, occipital view of skull. All $\times 4$.

Diagnosis. Microbrachomorph microsauro, possibly belonging to the family Brachystelechidae, differing from *Brachystelechus* and *Carrolla* in having extremely short and broad nasals that show no area of articulation for the premaxillae. Stapes apparently lacking stapedia foramen. Cultriform process of parasphenoid separated from sphenethmoid by wide gap.

Quasicaecilia texana sp. nov.

Text-figs 1-5

Derivation of trivial name. Refers to the state from which the type species was collected.

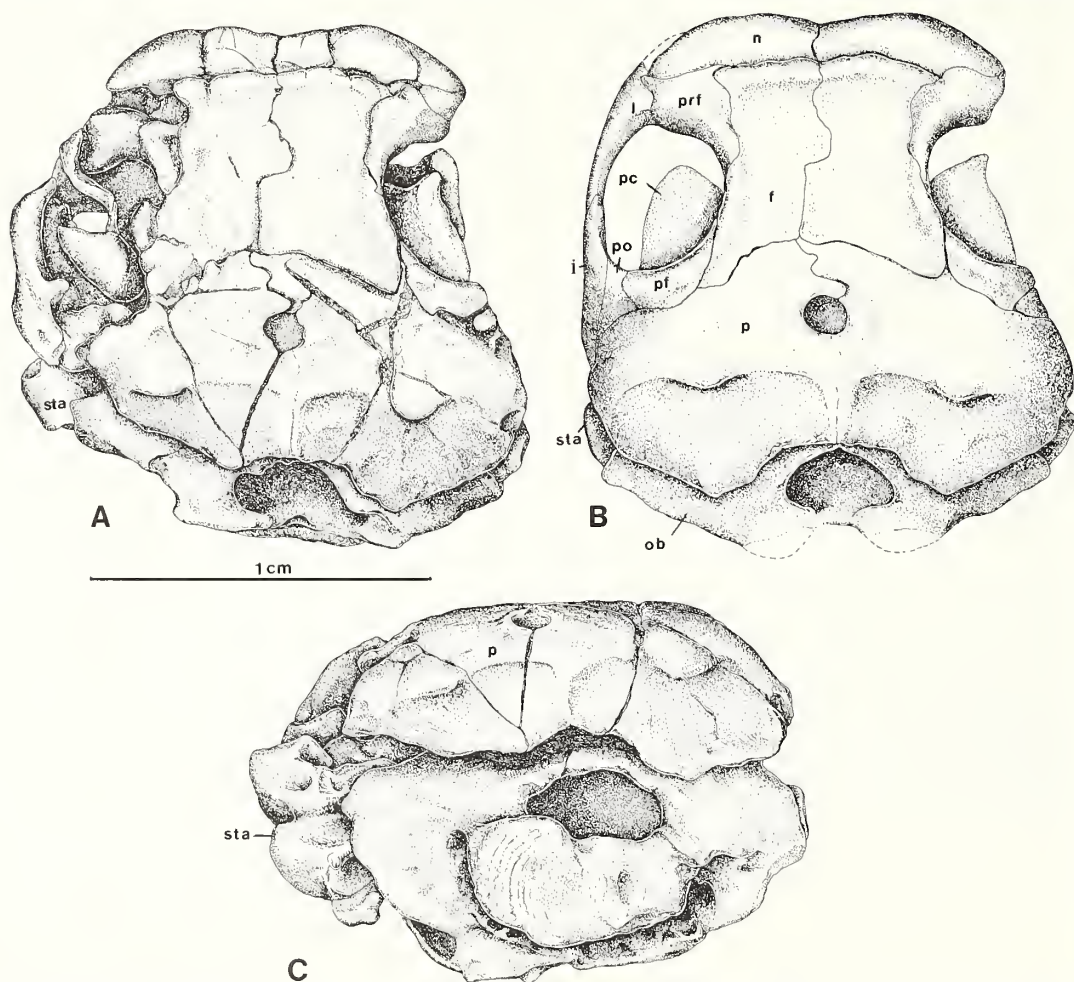
Holotype. United States National Museum (USNM) no. 22079.

Locality and horizon. ?Baylor County, Texas; Lower Permian ?Arroyo Formation.

Diagnosis. As for genus. This is the only recognized species.

Description. Both the orbital and pineal openings appear large relative to the length of the skull, as would be expected in a small animal. The orbits are protected by large saucershaped palpebral bones. The surface of the roofing bones is essentially smooth and shows no evidence of lateral line canals.

The pattern of the skull roof (Text-fig. 2) differs dramatically from that of all other Palaeozoic tetrapods.



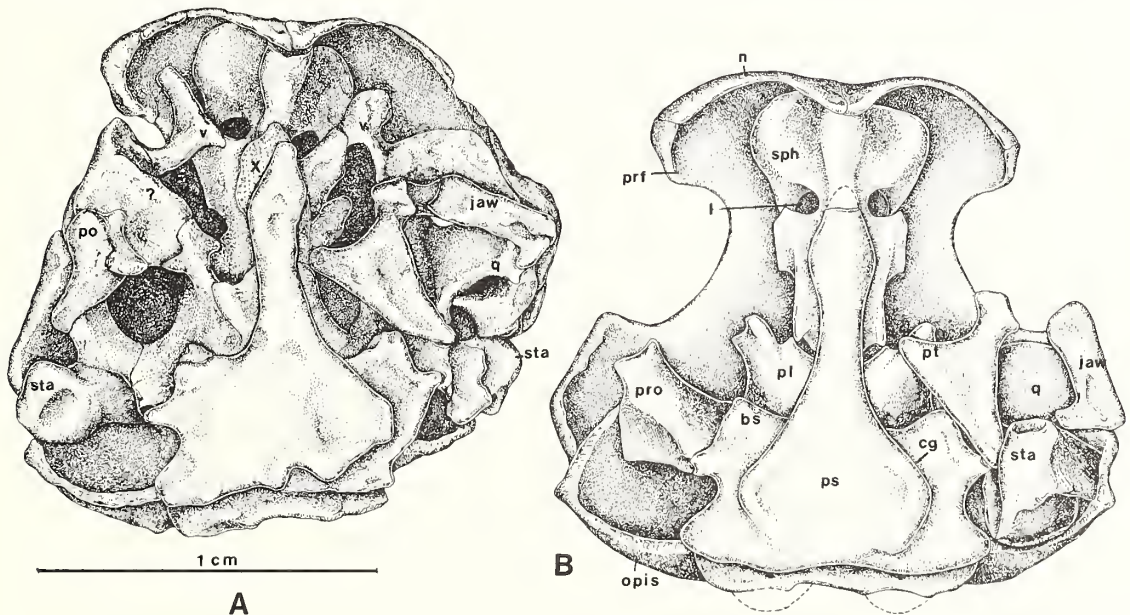
TEXT-FIG. 2. *Quasicaecilia texana*, type, United States National Museum, 22079. A, dorsal view of skull. B, reconstruction of skull in dorsal view. C, occipital view. All $\times 4.5$. Abbreviations: a, angular; ba, basicranial articulation; bo, basioccipital; bs, basisphenoid; c, coronoid; cg, groove for carotid artery; com, composite of posterior jaw bones; d, dentary; dp, dorsal process of stapes; ect, ectopterygoid; eo, exoccipital; f, frontal; f-p, frontoparietal; j, jugal; l, lacrimal; m, maxilla; n, nasal; ob, os basale; opis, ophisthotic; otic, position of otic capsule; p, parietal; pal, palatine; pc, palpebral cup; pca, palatine canal; pf, postfrontal; pl, pleurosphenoid; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sm, septomaxilla; so, supraoccipital; sp, splenial; sph, sphenethmoid; sq, squamosal; st, supratemporal; sta, stapes; syt, synotic tectum; t, tabular; t-sq, bone occupying position of tabular and squamosal; v, vomer; X, area of matrix left for support of cultriform process of stapes; ?, bone of uncertain identity; I, II, V, foramina for cranial nerves.

It consists primarily of very wide parietal bones, rectangular frontals, and wide and extremely short nasals. The nasals are rounded anteriorly to form the anterior margin of the skull. They extend ventrally so as to surround the area that would have been occupied by the nasal capsules. No bone occupies the position expected of the premaxillae at the anterior margin of the skull roof or palate. Since there is no area for their articulation with the nasals, it is probable that they were not solidly attached to the skull. There is no trace of postparietal bones. The parietals, as in modern caecilians, extend far posteriorly over the back of the braincase. Behind the pineal opening they appear fused at the midline where the bone forms a ridge that extends nearly to the margin of the foramen magnum between two areas that are recessed to receive the epaxial musculature. A transverse ridge on the parietals clearly demarcates the anterior limit of this musculature. On each side, the ridge is bowed posteriorly and slightly overlaps the occipital surface. There is no evidence of the large tabular bones that characterize tuditanomorph microsaurs.

The frontal narrowly enters the orbital margin between the pre- and postfrontals. All three bones form a wide medial margin to the orbit. The left postfrontal is missing, revealing a thick area of the parietal to which it was attached. On the right side, a small triangular remnant of the postorbital is retained in place between the postfrontal and the parietal. The remainder of the bone is broken off and appears in palatal view, with the lateral surface exposed medially. The entire bone is triangular in outline. The left jugal appears in more or less its natural position beneath the orbit. The remainder of the cheek region (Text-fig. 5) is badly crushed, making determination of its original configuration extremely difficult. The great size of the otic capsule indicates that the jaw articulation must have been far anterior in position. This is confirmed by the presence of the quadrate just behind the orbital opening. Presumably the squamosal occupied a narrow vertical area behind the jugal and wrapped around the quadrate posteriorly. The broken nature of the bone surface behind the jugal precludes determination of the presence or absence of the quadratojugal. The quadrate is the shape of a thickened vertical plate. The dorsal end is angled towards the posterior margin of the orbit. The lateral portion of the lower end forms a hemispherical condyle. More medially, the distal surface is broadly embayed for a distance that is as great as the width of the condyle. The medial edge is in contact with the quadrate ramus of the pterygoid. The shortness of the cheek and the large size and orientation of the quadrate indicate that the adductor chamber must have been very small, providing little space for jaw-closing musculature.

A thin crescent of bone above the distal end of the jugal may be the left palpebral cup. Beneath this is an area of bone that may be the lacrimal, although no opening for a lacrimal duct is evident. No trace of the maxillae can be identified.

A large triangular bone on the left side of the palatal area (Text-fig. 3) is identified as the pterygoid. Its



TEXT-FIG. 3. *Quasicaecilia texana*. A, palatal view of skull. B, reconstruction of palate; right side shows braincase with elements of palate and stapes omitted. $\times 4.5$.

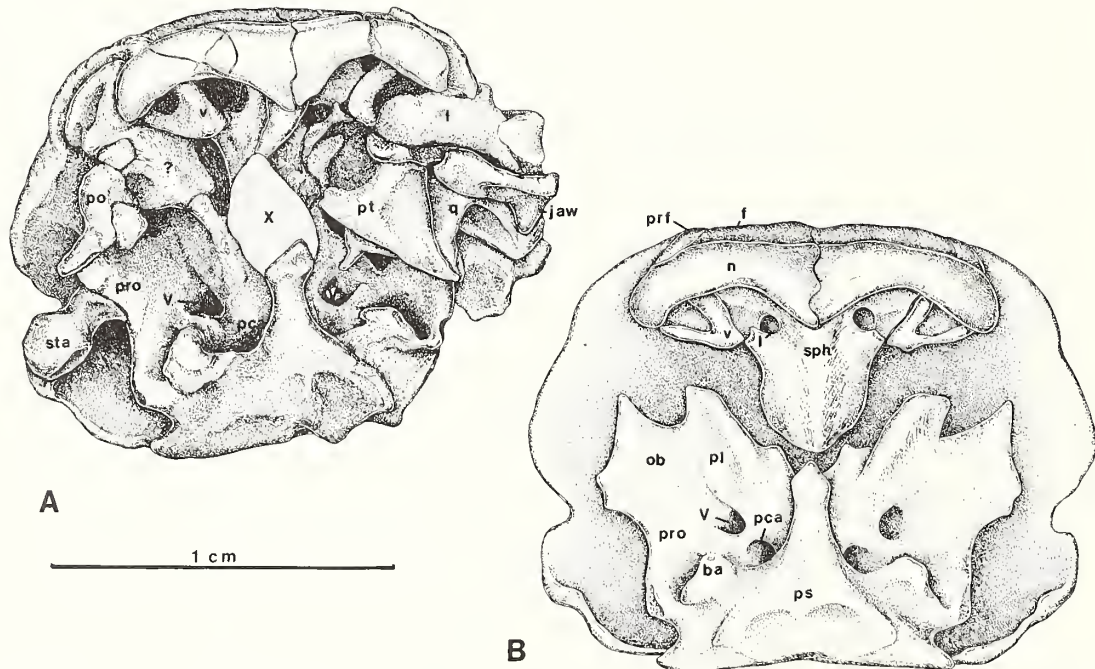
posterior end is in contact with the medial surface of the quadrate. Medially, it may have been in contact with a small unfinished surface of the prootic. The posteromedial surface of the bone shows no evidence of the basicranial articulation. Laterally, the bone angles sharply dorsally. A similar dorsal projection was noted in *Carrollia* by Langston and Olson (1986). The anterior surface of the bone is broadly concave. This implies an unusual outline for the interpterygoid vacuities, but this area might have accommodated retraction of the relatively large eyes. Anterolaterally, the pterygoid ends in an enlarged surface that appears to terminate in an oval area of articulation. This might have attached to the ectopterygoid or palatine.

Bone is visible on the right side between the orbit and the base of the braincase, but none of the surfaces is sufficiently well preserved to permit identification. Anteriorly, on both sides, are smaller bones with two rami meeting at nearly right angles. They are logically identified as the vomers. They lie adjacent to the sphenethmoid; presumably they were displaced from a more ventral position.

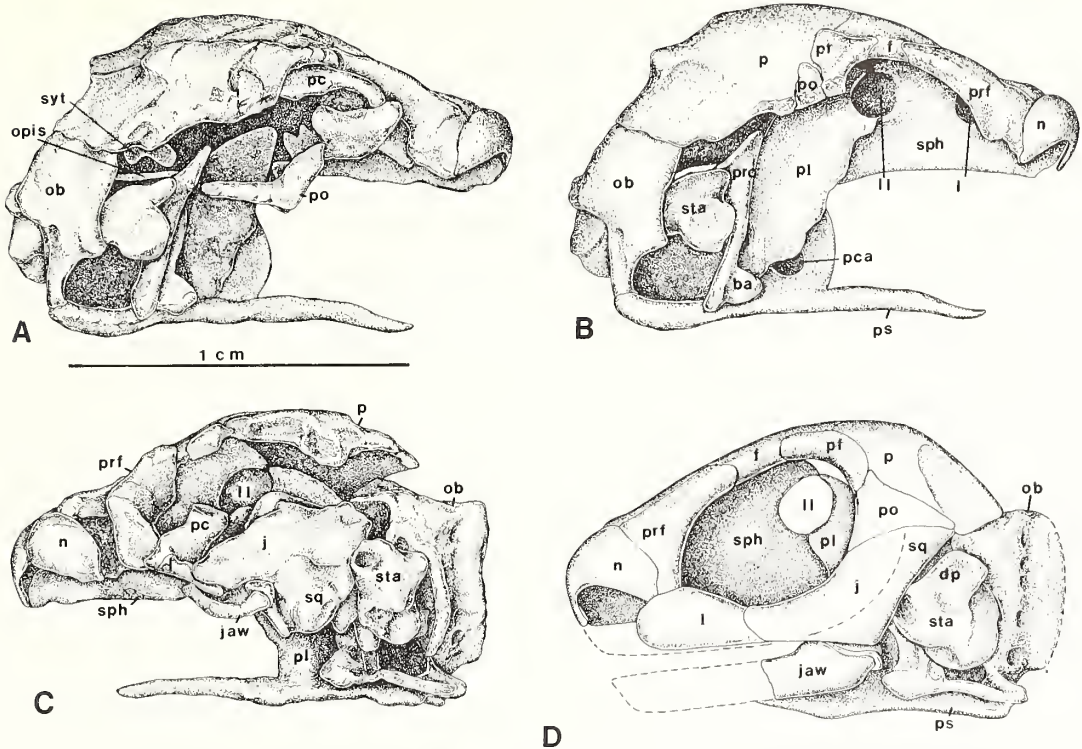
Above the scattered and difficult to identify palatal elements is a heavily ossified braincase (Text-figs 4 and 5). Its degree of ossification is matched by that of aistopods, but its structure is unique among Palaeozoic tetrapods. The braincase consists of two major elements, the anterior sphenethmoid, broadly comparable to the sphenethmoid of Palaeozoic labyrinthodonts, and the posterior otic-occipital complex. The latter incorporates all the bones recognized in other Palaeozoic tetrapods, fused into an essentially unipartite structure. The basioccipital, exoccipitals, supraoccipital, basisphenoid, laterosphenoids (or pleurosphenoids), opisthotics, prootics and parasphenoid are all fused without trace of sutures, except possibly the dorsal contact between the opisthotic and prootic. The resulting structure vaguely resembles the os basale of eacilians.

The articulating surface of the basioccipital and exoccipitals is lost, but would have been very wide as in typical microsaur. The ventrolateral surface of these bones is deeply grooved just above the area of the parasphenoid. This groove is irregularly pitted, probably for insertion of hypaxial musculature to lower the head. Nerves X–XII presumably exited in this area, but their foramina cannot be differentiated with certainty from the other pits.

One of the most striking features of this tiny skull is the relatively enormous size of the otic capsules and stapes. The otic capsules extend to the lateral extremities of the skull as preserved. The fenestrae ovales appear huge in ventral view. They are almost 4 mm in dorsoventral extent. Their configuration differs somewhat on the two sides. On the right side the opisthotic rim extends further laterally than the prootic. On the left side



TEXT-FIG. 4. *Quasicaecilia texana*. A, oblique anteroventral view of skull. B, reconstruction of skull in anteroventral view. Most palatal elements have been omitted to expose braincase. $\times 4.5$.



TEXT-FIG. 5. *Quasicaecilia texana*. A, right side of skull. B, restoration of the skull in right lateral view, with cheek removed to show braincase. C, left side of skull. D, restoration of skull in left lateral view; configuration of cheek is very speculative. Left and right sides have been independently restored. $\times 4.5$.

the condition is reversed. The left capsule is somewhat compressed from back to front. Posteriorly, the opisthotics and exoccipitals are continuous with the supraoccipital, which extends forward a short distance beneath the overlying parietals.

The stapes is present in association with the fenestra ovalis on both sides, but on neither side is it in natural articulation. On the left side, the foot plate of the stapes is in continuity with the margin of the prootic in a clearly unnatural position that suggests minor dissolution and redeposition of the calcium phosphate during preservation. Otherwise the bone appears to retain its natural configuration. The foot plate extends for slightly less than 3 mm in dorsoventral diameter. It is not possible to reconstruct its exact position in the fenestra, but there may have been a medial unossified gap, as in several microsaurs (Carroll and Gaskill 1978). The stem of the stapes is somewhat less than 2 mm in diameter and 4 mm in length including the base of the foot plate. The stem appears to point anteroventrally, and ends in a shallow depression that may have been continued in cartilage. No stapelial foramen is evident. From the stem extends a broad but thin dorsal process that is almost parallel with the surface of the foot plate. What appears to be the right stapes is a simple columnar structure. It is about the size of the stem of the left stapes. Damage prior to burial may have led to the loss of the dorsal process and the margins of the foot plate.

Above the fenestra ovalis, the area of the inner ear continues to the skull roof. Medially, a further ossification is encountered that is not solidly fused to other elements. It is tentatively identified as an ossification of the synotic tectum. It bears grooves that may have accommodated the dorsal portion of the vertical semicircular canals. In several microsaurs (*Pelodiosotis*, *Pantylus*, and *Rhynchonkos* [*Goniorhynchus*]), the supraoccipital continues anteriorly to incorporate the area of the synotic tectum, but this area appears to be separate in *Quasicaecilia*. In *Microbrachis*, in contrast, there is apparently no supraoccipital, but there is a more anterior ossification that may represent the synotic tectum. DeBeer (1937) recognized the presence of both a posterior tectum, which may ossify as the supraoccipital, and a more anterior synotic tectum in all major vertebrate

groups, but noted that their expression in individual species is extremely variable and appears to have little taxonomic significance.

In anterior view, the prootic appears as a nearly vertical sheet of bone that forms the anterior wall of the otic capsule. Ventrally, it is continuous with the parasphenoid-basisphenoid area. Just above the parasphenoid plate, a short area of unfinished bone is evident on both sides. It may have been in contact with the quadrate ramus of the pterygoid. Above this area the margin of the prootic is inflected posteriorly and somewhat medially into the fenestra ovalis.

Posteriorly, the prootic terminates some distance below the skull roof, along a line that corresponds to the dorsal margin of the fenestra ovalis. A very thin flange of bone, continuous with the surface of the right stapes, may represent the anterior extension of the opisthotic towards the prootic in this area. Anteriorly, the prootic extends further dorsally, narrowing to a point laterally. Anteromedially the prootic is notched for the prootic foramen, an opening formed jointly with the pleurosphenoid. The opening, clearly visible with minimal distortion on both sides, is approximately 0.9 mm in diameter, which is strikingly small relative to the other cranial dimensions.

At the base of the braincase, at the anterior margin of the posterior plate of the parasphenoid, are the basicranial processes which extend anteriorly as shelflike structures. No specific area of articulation is distinguished by unfinished bone surface. The adjacent margin of the pterygoid does not show a specialized area for the articulation between the braincase and the palate. Just anterior to the basicranial articulation are foramina that are comparable in position to those in caecilians which serve for the palatine arteries.

Anterior to the prootic, the area of the pleurosphenoid, most completely visible on the right side, forms the lateral wall of the braincase. It rises nearly vertically from the area of the basisphenoid-parasphenoid, and extends as a narrow sheet of bone to within less than 2 mm of the underside of the skull roof. It is lower posteriorly, where it is continuous with the prootic, and rises anteriorly. On the left side, it can be seen to form the posterior margin of a large opening for the optic and possibly the oculomotor nerves. The opening is about 2 mm in diameter, substantially larger than the opening for the Vth nerve. The pleurosphenoid forms the anterior margin of the oticoccipital portion of the braincase. Ventrally, there is a wide gap above the parasphenoid. Dorsally, the pleurosphenoid lies lateral of the sphenethmoid, apparently without being in sutural contact.

The anterior extent of the pleurosphenoid, beyond the level of the basicranial processes, would appear to preclude the origin of the rectus eye muscles from a retractor pit in the position of that structure in amniotes and anthracosaurian labyrinthodonts, as described by Clack and Holmes (1988). The high degree of specialization of all aspects of the braincase makes specific comparison with any labyrinthodonts difficult, however.

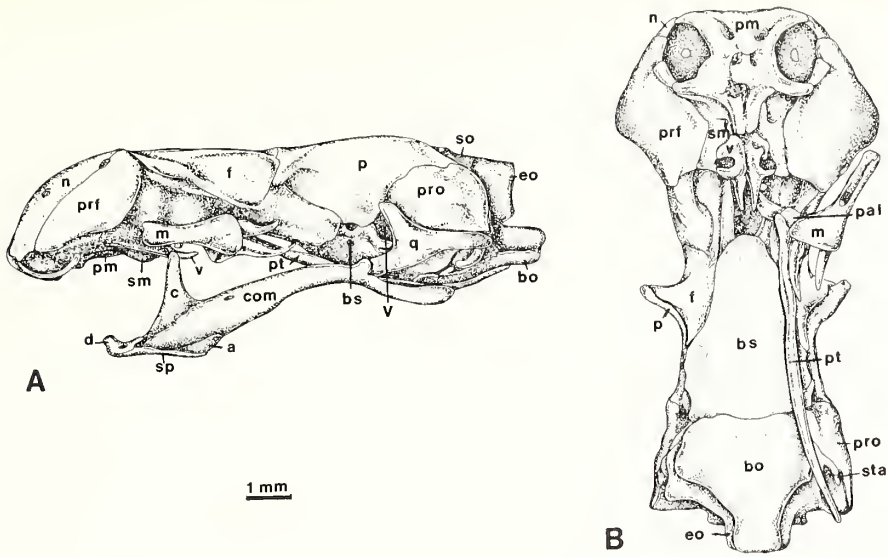
The posterior portion of the braincase is covered ventrally by the plate of the parasphenoid, indistinguishably fused to the overlying endoskeletal elements. The parasphenoid is marked on the left side by a strong ridge that formed the medial border of a groove for the carotid artery. This ridge is missing on the right side. The cultriform process of the parasphenoid extends forward like a dagger. It may have angled somewhat dorsally, but could not have underlain the sphenethmoid directly.

The sphenethmoid is visible in ventral and lateral views as a tubular structure extending anteriorly from the area of the pleurosphenoid to the front of the nasals. It appears to be closely appressed to the underside of the skull roof, beneath the frontals. Posteriorly, it forms the upper border of the foramen for the optic nerve, where it lies slightly medial to the pleurosphenoid. In contrast with caecilians, these bones do not abut against one another. Rather, the sphenethmoid appears to fit within the anterior borders of the pleurosphenoids.

The sphenethmoid is pierced laterally by relatively large foramina for the olfactory nerve. The anterior end of the bone is dorsoventrally compressed but widened laterally behind the front of the skull. This portion of the bone presumably served primarily as a structural brace since the foramina for nerve I exit more posteriorly, rather than at the end of the bone. The ventral border of the sphenethmoid is broadly rounded, but ends well above the cultriform process of the parasphenoid. In this it differs from other microsaurians in which the sphenethmoid is ossified, where it appears to be supported by the parasphenoid ventrally. The sphenethmoid is very incompletely ossified in early amniotes, but in genera in which it is preserved, there is also a wide gap between it and the cultriform process of the parasphenoid. The remainder of the braincase in this genus and early amniotes is so different that this one similarity is not thought to be taxonomically significant.

On the left side, just anterior to the otic capsule, is the posterior end of the lower jaw. The articular bone is in articulation with the condyle of the quadrate. Anteriorly it extends dorsally against the surface of the quadrate. Medially, the articular extends well beyond the remainder of the jaw. There is no retroarticular process. The anterior, tooth-bearing portion of the lower jaw is not preserved.

With no evidence of the postcranial skeleton, there is little basis for establishing the general adaptation of



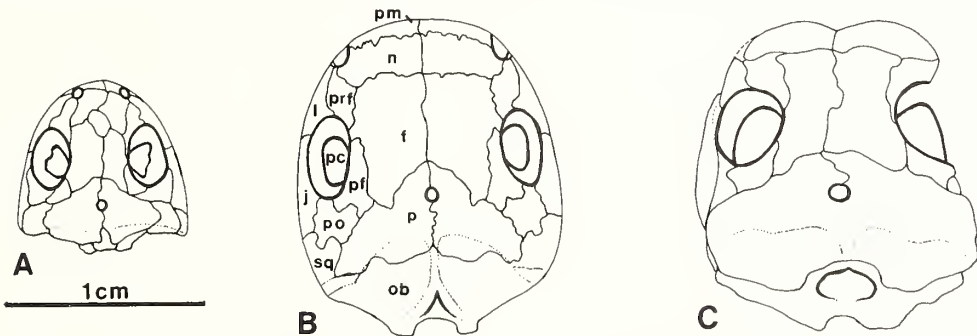
TEXT-FIG. 6. A, B, skull of the burrowing snake *Typhlops punctatus* in lateral and ventral views, modified from Parker (1977); small size of prootic foramen may be associated with reduction in size of jaws and dentition.

this species. A somewhat analogous modification of the cranial anatomy can be seen in burrowing typhlopids snakes (Text-fig. 6) in which the marginal jaw elements have lost their tooth-bearing role, and are much modified. As in caecilians, the fusion of the otic-occipital elements of the braincase might be attributed to a burrowing habitus, but such fusion did not occur in primitive burrowing snakes.

DISCUSSION

Taxonomic position

Despite the loss of their articulating surfaces, the great width of the exoccipitals and basioccipital in *Quasicaecilia* indicates the presence of wide condyles as in typical microsaur. The pattern of the bones of the skull table resembles that of members of the Microbrachomorpha in the great width of the parietals and the progressively smaller size of the frontals and nasals. The greatest resemblance is to the previously described members of the family Brachystelechidae (Carroll and Gaskill 1987; Langston and Olson 1986) (Text-fig. 7). In both *Brachystelechus* and *Carrolla*, the



TEXT-FIG. 7. Skulls of the three genera assigned to the Brachystelechidae. A, *Brachystelechus*. B, *Carrolla*. C, *Quasicaecilia*.

parietals overlap the occipital surface, and the tabulars are either greatly reduced or entirely missing. All three genera have very wide skulls and possess palpebral cups.

Quasicaecilia resembles *Carrolla* in the high degree of ossification of the braincase; the cranial endoskeleton is not known in *Brachystelechus*. *Quasicaecilia* definitely differs from *Brachystelechus* in the shortness of the nasals, and from *Carrolla* by the absence of sutural attachment between the nasals and the premaxillae. *Quasicaecilia* also differs from *Carrolla* by the absence of a stapedial foramen and the separation of the sphenethmoid and the cultriform process of the parasphenoid.

The degree of specialization of these three genera appears to correspond with their stratigraphic succession. The relative age of specimens from the European Rotliegend succession is subject to continuing dispute, but Boy (1987) suggested that the horizon from which *Brachystelechus* was collected is roughly equivalent to the North American Admiral Formation. *Carrolla* comes from the Belle Plains Formation. *Quasicaecilia* is said to come from the Arroyo Formation, but this is indicated with a question mark on the label. No other described group of Palaeozoic tetrapods shares more derived characters in common with *Quasicaecilia* than do the previously identified members of the Brachystelechidae.

Affinities between goniorhynchid microsaur and caecilians have been postulated on the basis of derived features of the braincase, several of which are also exhibited by *Quasicaecilia* (Carroll and Currie 1975; Walsh 1987; Jenkins and Walsh, in preparation). The fusion of the posterior portion of the braincase into a unitary os basale, the large size of the otic capsule, the presence of a large pleurosphenoid, the anterior position of the jaw articulation and the loss of dermal bones at the back of the skull table are features expected in the ancestors of caecilians (Walsh 1987). On the other hand, in all caecilians, premaxillae make up the anterior margin of the skull. Caecilians and their putative ancestors, the microsaure family Goniorhynchidae, are characterized by the small size of the orbits, in contrast with their large size in *Quasicaecilia*. Caecilians maintain the primitive pattern of having the sphenethmoid supported by the parasphenoid, in contrast with the derived condition seen in *Quasicaecilia*.

Many of the features in which *Quasicaecilia* resembles modern caecilians may be associated with small size and so do not constitute a strong basis for assuming close relationship.

Anatomical significance

The most interesting features of this specimen are the anatomical peculiarities, especially of the braincase. Among the most conspicuous are the great size of the otic capsule and stapes, but the relative size of the orbits and the configuration of the nasal region are also unusual.

The relatively large size of the sensory structures can be attributed primarily to the absolutely small size of the skull. The great importance of the sensory structures and the braincase in constraining the proportions of other features of the skull in small tetrapods was discussed in a compelling fashion by Hanken (1983, 1984) in his study of miniaturization in salamanders of the genus *Thorius*.

Although some species of modern frogs, salamanders, and caecilians are even smaller than this specimen, it is among the smallest Palaeozoic amphibians. Comparative dimensions of the braincase and sense organs of *Quasicaecilia* and other small tetrapods are given in Table 1.

In *Quasicaecilia* and other Palaeozoic tetrapods, the dimensions of the bony otic capsule and braincase can be measured directly. It is assumed that, as in other small tetrapods, the circumference of the eyeball closely matches that of the bony orbital margin. This is confirmed in many small Palaeozoic amphibians by the extent of the sclerotic ring which fills most of the orbital space. The size of the nasal capsule is more difficult to estimate. It is never ossified in Palaeozoic tetrapods (in contrast with their rhipidistian relatives). In some species, the extent of the capsule can be judged from impressions in the undersurface of the overlying dermal bones, but this area is only rarely exposed. In animals with small skulls, the probable size of the nasal capsule can be roughly estimated by the space available between the front margin of the skull and the anterior limit of the orbit, taking into consideration the position of the internal and external narial openings. In *Quasicaecilia*, the area of the nasal capsules appears to be outlined by the nasal bones that curve over the front

TABLE 1. Cranial dimensions of Palaeozoic and modern tetrapods. Area of sensory capsules and braincase are expressed as a percentage of the total skull area following the model of Hanken (1983). Measurements of *Thorius* and *Pseudoeurycea* from Hanken (1983). Measurements of *Ambystoma* from specimens in Redpath Museum. Measurements of fossils from literature cited in text.

Species	Skull length (mm)	Olfactory capsule (%)	Optic capsule (%)	Otic capsule (%)	Braincase (%)
<i>Quasicaecilia texana</i>	15	11	13	20	18
<i>Cardiocephalus sternbergi</i>	16	5	4	14	14
<i>Brachyectes elongatus</i>	18	7	9	19	23
<i>Rhynchonkos stovalli</i>	18	8	9	13	18
<i>Doleserpeton annectens</i>	11	8	25	9	18
<i>Tersomius texensis</i>	58	5	16	5	13
<i>Phlegethontia longissima</i>	23	6	15	12	20
<i>Thorius pennatulius</i>	3.3	14	27	17	37
<i>Pseudoeurycea goebeli</i>	10.6	17	18	11	23
<i>Ambystoma jeffersonianum</i>	15	9	11	11	22
<i>Ambystoma tigrinum</i>	19	14	12	11	15

margin of the skull, inclosing a circular space lateral to the opening for the olfactory tract. The extent of the nasal capsule is the most difficult of the sensory organs to estimate, but judging from modern salamanders, it is probably the least important in controlling the proportions of the skull.

Fortunately, the measures of the relative area of the entire skull and the sensory capsules used by Hanken can be compared directly with small Palaeozoic amphibians. The adult salamander specimens he measured range from 3.3 mm (*Thorius pennatulius*) to 10.6 mm (*Pseudoeurycea goebeli*) in skull length – all smaller than *Quasicaecilia*. Study of living forms shows that there is slight positive allometry shown by the nasal capsules, but strong negative allometry for the relative size of the otic capsule, eye, and braincase. These allometric relationships apply to both ontogeny within a particular species and to comparison between adults of different size within related groups.

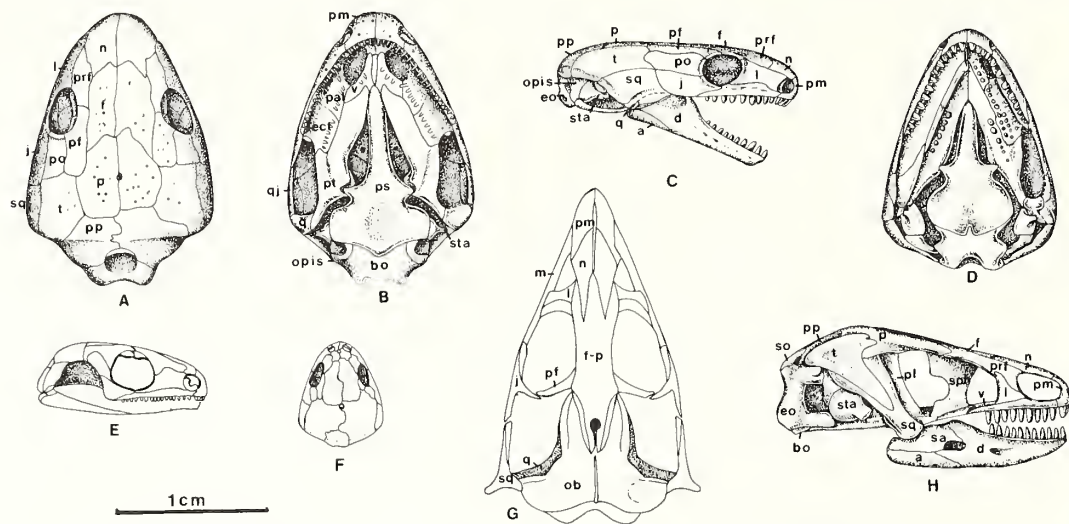
The relative size of the nasal capsules, eyes, and braincase of *Quasicaecilia* are similar to those of salamanders measuring 15 and 19 mm in skull length, but are much smaller than those of the specimens examined by Hanken. In contrast, the otic capsules of *Quasicaecilia* are substantially larger than those of even the smallest salamander measured by Hanken, and approximately twice the size of those in salamanders in which the skull length is comparable to that of *Quasicaecilia*. In fact, nearly all the Palaeozoic specimens that were examined have very large otic capsules. The relatively large size of the semi-circular canals in Palaeozoic vertebrates has been discussed previously (Bernacsek and Carroll 1981). Several hypotheses have been advanced, but the specific physiological reason(s) for larger inner ear structures in early vertebrates has not yet been established. Presumably, early Palaeozoic tetrapods inherited this condition from their immediate ancestors among the rhipidistian fish. Although the data remain limited, it appears likely that the size of the otic capsule is an even more important factor in controlling the configuration of the skull in Palaeozoic tetrapods than it is in modern genera.

The otic capsules in *Quasicaecilia* dominate the back of the skull and extend to the margin of the cheek. As a result of their large size, the jaw suspension occupies a more anterior position and the adductor chamber is very small. This pattern is closely reminiscent of the early developmental stages of modern amphibians (DeBeer 1937). Ossification presumably occurred in an individual retaining essentially embryonic cranial proportions. The small size of the prootic foramen indicates a small Vth nerve, and reduced importance of the adductor jaw musculature. This, however, cannot be explained as a direct result of small skull size, since modern caecilians have skulls of even smaller size, and yet retain a large foramen for the Vth nerve.

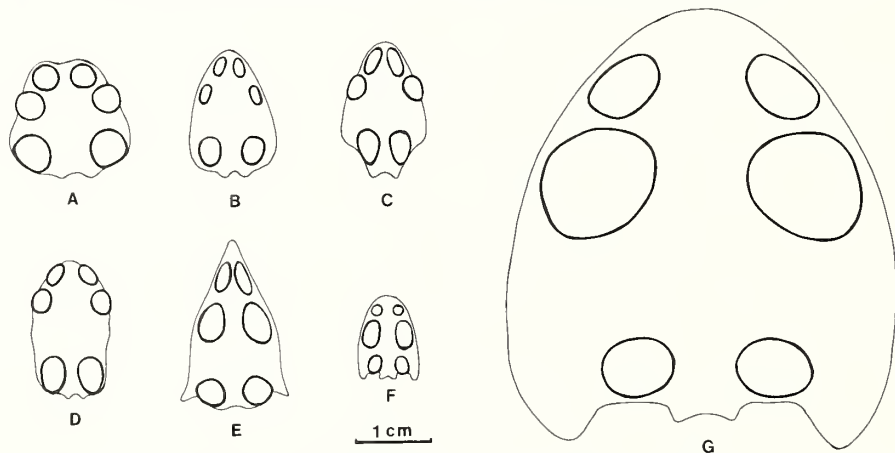
The relatively anterior position of the orbits may also be attributed to the large size of the otic

capsules. In contrast, the configuration of the nasal bones and the absence of articulating surfaces for the premaxillae probably cannot be attributed simply to small size since the nasals are relatively long in the related genus *Brachystelechus*, which has an even shorter skull (estimated length 8.4 mm). *Carrollia*, a member of the same family, is approximately 15 mm long and has short nasals, but suturally attached premaxillary bones. The separation of the cultriform process from the sphenethmoid cannot be directly attributed to small size either, since the bones are in their normal position in *Carrollia*.

Examination of other genera (Text-figs 8 and 9) suggests that constraints related to the sense

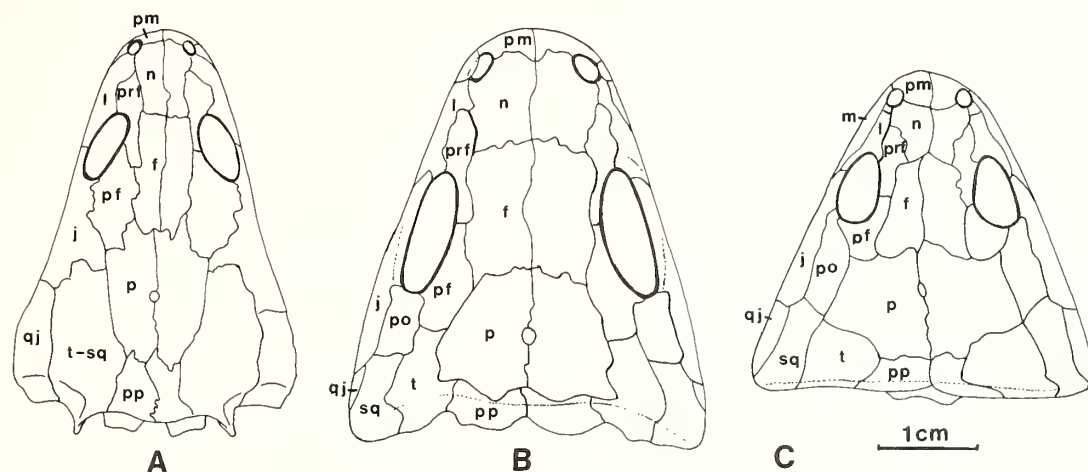


TEXT-FIG. 8. Skulls of amphibians less than 3 cm in length, all of which have large otic capsules and show modification in the position of the jaw articulation, adductor chamber and/or bones of the skull table. All $\times 2$. A-F, microsaur; A, B, *Rhynchonkos* [*Goniorynchus*], in dorsal and palatal views; C, D, *Cardiocephalus sternbergi*, lateral and palatal views; E, *Hapsidopareion*, in lateral view. F, *Odonterpeton*, in dorsal view. G, the aistopod *Phlegethontia*. H, lateral view of the lysorophid *Brachydectes elongatus*. (A-F, from Carroll and Gaskill 1978; G, from McGinnis 1967; H, from Wellstead 1985.)



TEXT-FIG. 9. Outline drawings of the skulls of small Palaeozoic tetrapods showing the areas of the sensory capsules. Drawn to a common scale. A, *Quasicaecilia*. B, *Cardiocephalus sternbergi*. C, *Rhynchonkos*. D, *Brachydectes elongatus*. E, *Phlegethontia*. F, *Doleserpeton*. G, *Tersomius*; in this genus the extent of the nasal and otic capsules have been established by serial sectioning.

organs may have a more general significance in determining the cranial anatomy of small animals belonging to a variety of Palaeozoic groups. The size of the orbits is extremely variable in Palaeozoic tetrapods, and the dimensions of the nasal capsules are difficult to estimate, but the otic capsule appears to retain a nearly constant size in small adults (Text-fig. 8) – from 13% to 20% of skull area in skulls less than 2 cm in length. Since the capsules extend nearly to the lateral margin of the skull, the area of the jaw articulation and/or adductor chamber is typically much modified.



TEXT-FIG. 10. Skull roof of A, *Adelogyrinus*; B, *Asaphstera*; C, *Microbrachis*. Drawn to the same scale. The skulls of these genera are all greater than 3 cm long, and none shows evidence of modification resulting from a large otic capsule.

In the earliest and/or most primitive known members of the Adelogyrinidae and the two Microsauria suborders, Tuditanomorpha and Microbrachomorpha, the skull is still three centimeters or more in length (Text-fig. 10). The otic capsules are not known in these forms, but they would not be expected to be of sufficiently large size to require accommodation in the area of the jaw articulation or adductor chamber. In contrast, this has occurred separately within several microsauro families, and in the Lysorophia, Nectridea, and Aistopoda.

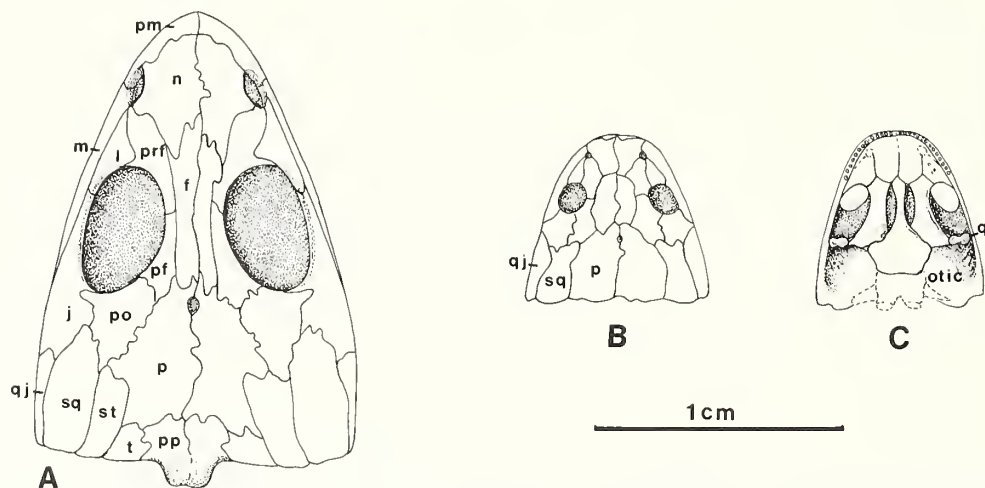
Members of the tuditanomorph microsauro families Goniiorhynchidae, Hapsidopareiontidae, and Gymnarthridae, and the microbrachomorph *Odonterpeton triangularis* have skulls less than three centimeters in length. In the Goniiorhynchidae and small gymnarthrids, the jaw articulation is anterior to the otic capsule. The jaw articulation remains in a posterior position in the Hapsidopareiontidae, but in some members of this family the cheek region is emarginated, enabling the jaw musculature to expand beyond the confines of the restricted adductor chamber. These three families retain the primitive pattern of the bones of the skull table. In contrast, they are much modified in *Odonterpeton*, in which the skull of the only known specimen is 6.7 mm in length. In this genus, the parietals are greatly expanded and the postparietals are reduced to a tiny median element.

However, there are apparent exceptions to the association between small skull size and modification of the otic region in two microsauro genera. Within the Hapsidopareiontidae, *Saxonerpeton* is known from several skulls, none more than 1.5 cm in length, but the jaw suspension and cheek region do not appear modified from the pattern of larger microsaurs. Although all the specimens of *Saxonerpeton* are moderately well ossified, they may not be of adult size. Several species of gymnarthrid microsaurs are known from the Lower Permian. They show a progressive shift in the position of the jaw articulation with decreasing skull size. In *Euryodus*, with a skull approximately 3.5 cm in length, the jaw articulation is posterior in position: essentially in the plane of the occiput. In *Cardiocephalus sternbergi*, the skull is approximately 1.6 cm in length, and the jaw articulation has shifted forward, 30% of the skull length (Carroll and Gaskill 1978, fig. 105). On

the other hand, a well-preserved skull of *Sparodus*, from the Upper Pennsylvanian, with a skull 3.3 cm long (Carroll 1988) also has the jaw articulation far forward. This may be attributed to a change in jaw mechanics associated with the large size of the marginal and palatal dentition, rather than to small size.

Among other lepospondyls, all members of the Lysorophia possess relatively small skulls, dominated by sensory structures. The jaw articulation is anterior to the otic capsule and the adductor chamber is open laterally (Wellstead 1985).

The configuration of the skull of aistopods (McGinnis 1967; Thomson and Bossy 1970; Wellstead 1982) is highly modified. All have an open cheek, although the jaw articulation retains a relatively posterior position in large individuals. In none of the described species is the adult skull less than 2 cm long, but the bones of the braincase are fused to one another and the otic capsules are large in *Phlegethontia*.



TEXT-FIG. 11. Nectridean skulls. A, *Ptyonius marshii* (from Bossy 1976). B, C, skull roof and palate of *Scincosaurus crassus* (from Milner 1978). Drawn to the same scale.

Ptyonius marshii (Text-fig. 11) is an early nectridean that has a skull shape resembling that of primitive labyrinthodonts except for the loss of the squamosal embayment, and retains all the primitive roofing bones except the intertemporal. The largest known skull is only 19 mm long. In contrast with some other nectrideans, the carpals and tarsals are not ossified, which suggests that even the largest specimens may not have reached maturity. *Scincosaurus crassus*, from the Upper Carboniferous of Czechoslovakia, has the smallest skull among possibly mature nectrideans – approximately 7 mm in length. What is known of the otic capsule indicates very large relative size, and the jaw articulation is displaced anteriorly. Postcranial remains are known of a related species from North America, but they indicate an animal only twice the size of the European form (Milner 1980).

As in modern salamanders (Hanken 1984), the relatively small size of all animals termed lepospondyls may contribute to the loss of dermal bones from the pattern seen in early labyrinthodonts. The fact that different bones are absent in microsaur, nectrideans, and adelogyrinids suggests that they were lost independently in different lineages, each of which separately reduced their body size. If all animals termed lepospondyls evolved from a single common ancestor that had already reduced its skull size significantly, one would expect to observe a common pattern of bone reduction.

A general problem in interpreting the significance of small size among Palaeozoic tetrapods is the near impossibility of knowing whether the available specimens are of adult size. Frogs and

salamanders, whose egg size is constrained to less than 10 mm in diameter by the absence of extra-embryonic membranes (Carroll 1970), may increase their cranial dimensions many fold before reaching adulthood. This was presumably the case for Palaeozoic amphibians as well (Boy 1987). Since all amphibians are small at hatching, it is presumably the adult size that imposes the primary constraint on the dimensions of the sensory capsules. Only measurements of adults are hence of significance in evaluating the quantitative effects of small size. Unfortunately, there is no objective way of establishing whether an individual specimen is an adult. Broadly speaking, large tetrapods show progressive ossification as they approach adulthood, but species with very small adult size may become heavily ossified at a much earlier growth stage (Hanken 1982). Hence, extensive ossification of the ends of the limb bones and the braincase may be evidence that the specimen in hand represents a species that reaches maturity at small size, but not necessarily that this particular specimen is of adult dimensions.

None of the genera recognized as labyrinthodonts shows modification of the skull adjacent to the otic region that can be attributed to small size. Many tiny individuals have been described (Boy 1987) but all appear to be larvae or later immature stages. Bolt (1969, 1977) proposed that the dissorophoid labyrinthodont *Doleserpeton* might be close to the ancestry of the modern 'lissamphibian' orders. Milner (1988) argued that small size was an important factor in the origin of frogs, salamanders, and caecilians. The skull of *Doleserpeton*, although little more than 1 cm in length, retains the proportions of larger dissorophoid amphibians, and the otic capsule occupies no more than about 9% of its area, much less than that of *Quasicaecilia* and other small 'lepospondyls'.

Bolt (1979) has suggested that the material of *Doleserpeton* from Fort Sill might represent juvenile individuals of a genus resembling *Tersomius*, which reached a skull length of approximately 6 cm. The apparently small area of the otic capsule supports this interpretation. Even if *Doleserpeton* does belong to an assemblage that is the sister group of frogs and possibly salamanders, most of the osteological features that are characteristic of the modern orders must have evolved subsequently, presumably in relationship to significant reduction in adult skull size.

Acknowledgements. I wish to thank the Division of Vertebrate Paleontology of the United States National Museum for the long-term loan of the type of *Quasicaecilia*. The final impetus to complete this study resulted directly from Robert Purdy's request for the return of this specimen. Many drawings of this specimen were carefully executed by Mrs Pamela Gaskill during the course of its preparation. Her artistry and patience are much appreciated. Photographs of this very difficult material were prepared by Mr Murray Sweet. Funds for this study were provided by the Natural Sciences and Engineering Research Council of Canada. Thanks are also due to Drs Green, Holmes and Sues who read early drafts of the manuscript.

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Typescript received 24 July 1989
Revised typescript received 12 January 1990

THE EYES OF LOWER CAMBRIAN EODISCID TRILOBITES

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ABSTRACT. The oldest known well-preserved trilobite eyes are described in the Lower Cambrian eodiscids *Neocobboldia chinlinica* Lee and *Shizhudiscus longquanensis* S. G. Zhang and Zhu, the latter being slightly older. The material, from south central China, is preserved as moulds or by partial replacement in phosphate, and gives fine details of lens structure. *Shizhudiscus* eyes have biconvex lenses, polygonal and closely packed as in normal holochroal eyes, whereas those of *Neocobboldia* have round, separated lenses, and compare with Middle Cambrian eodiscid eyes previously described as 'abathochroal'. The validity of 'abathochroal eyes' as a separate eye-type is discussed. The lenses of *Neocobboldia*, like those of some phacopids, conform to the ideal model of an aplanatic lens originally described by Des Cartes. Ontogenetic changes in the eyes are described for both species. These show that the programmes for growth of the visual surface and lens emplacement are separate and that the two sometimes got out of phase. The eyes of eodiscids are similar enough to those of other trilobites to suggest that this group is truly trilobitan. They also indicate how advanced the visual organs were at this early stage in trilobite history.

MOST trilobites bear a pair of laterally placed compound eyes, which are of particular interest because the trilobite eye is the most ancient visual system so far known. Although well-preserved trilobite eyes showing details of structure are comparatively rare in the fossil record, it has proved possible to build up a fair understanding of their structure and function. Following the initial studies of Clarke (1889) and Lindström (1901), two types of eye, holochroal and schizochroal have been recognized; a third type, abathochroal, was proposed by Jell (1975) for Cambrian eodiscids. Recent work is summarized by Clarkson (1975, 1979) and Miller and Clarkson (1980).

Schizochroal eyes are believed to have been derived from a holochroal-eyed ancestral type and holochroal eyes are the earliest to appear in the fossil record. But although the record of different kinds of trilobite eyes in the Ordovician and later is good, our knowledge of Cambrian eyes is sparse. In olenelloids, which are considered to be the earliest trilobites found in continuous rock sequences spanning Late Precambrian to early Cambrian times (e.g. in Morocco, North America and Siberia: Fortey and Whittington 1989), the eye may occasionally be preserved. For example, Palmer and Halley (1979, pl. 1, fig. 12) figured the visual surface in *Bristolia* and lenses have been reported in a few meraspides of *Olenellus gilberti* Meek from Alberta (Clarkson 1973, text-fig. 1). Eyes are also present in some Australian Middle Cambrian eodiscids described by Jell (1975), and in Upper Cambrian leptoplastine olenids described by Clarkson (1973). Occasional librigenae with eyes attached belonging to other Upper Cambrian taxa have been figured in various papers, though they have not been studied in detail. The principal reason for the paucity of trilobite eyes in the Cambrian was originally suggested by Öpik (1967): it is that in Cambrian trilobites the visual surface has been bounded by a circumocular suture, comprising the palpebral suture above the eye and the ocular suture below. This circumocular suture, according to Fortey and Whittington (1989), is a primitive character for all trilobites, including agnostoids and olenelloids, and loss of this suture by retention of the eye on the cheek is a derived character. When a trilobite whose eye was bordered by such a suture moulted or died, the visual surface would dehisce entirely and thus would not be preserved. This accords with the observations of Clarkson (1973) who showed that in the olenids the ocular suture became functional only in the adult, and that its retention in many later olenids, and in the vast majority of post-Cambrian trilobites, was due to paedomorphosis. Only because of this fortunate circumstance does the eye in more advanced trilobites remain attached to the librigena, so that it has a good chance of being preserved.

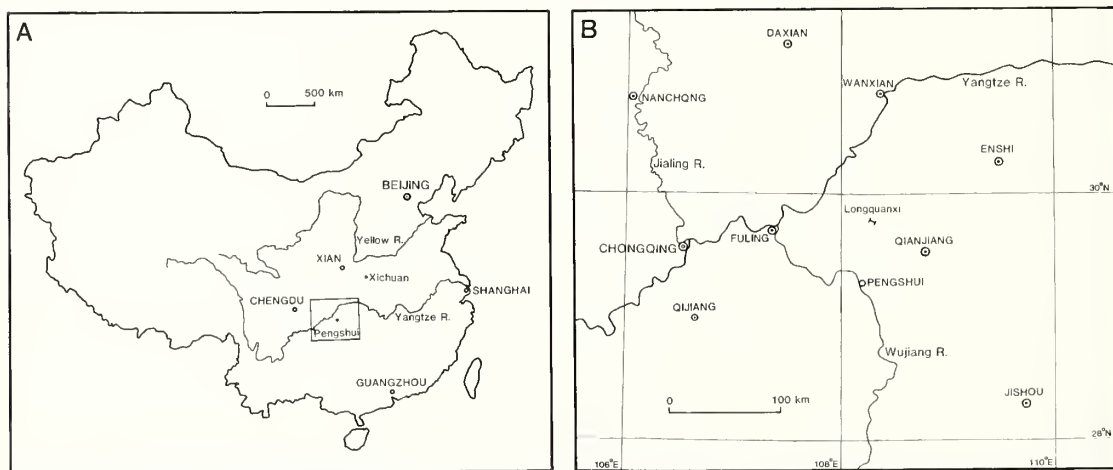
The Cambro-Ordovician Agnostida are generally considered as blind and lacking facial sutures, and ocular structures are known only in *Oculagnostus frici*, as reported by Ahlberg (1988). However, in the Cambrian eodiscid Family Pagetiidae Kobayashi, eyes and proparian sutures have been known for some time, though knowledge of these was limited until Jell's (1975) description of the eyes of *Pagetia* which he proposed as a new type of eye in trilobites – the abathochroal eye. Abathochroal eyes superficially resemble small schizochroal eyes, having a relatively small number of lenses (usually less than 100); these are biconvex and separated from one another. There is, however, no indication of deep intralensar sclera between the lenses, and in this respect they differ from schizochroal eyes proper. Jell (1975) suggests that each lens had its own separate corneal membrane, fixed to the intralensar area round the lens margin. If these differences can be confirmed, then the abathochroal eye can truly be regarded as a distinct type, but our material does not permit a final resolution of this issue.

The two eodiscid genera discussed in this paper both come from the Lower Cambrian of south central China but from different horizons. For both *Neocobboldia* and *Shizhudiscus* large numbers of phosphatized specimens with fine details of structure, and representing several growth stages, have been freed from the enclosing limestone by etching with acid. *Neocobboldia* is restricted to the Canglangpu Stage. Its eyes share a number of distinguishing features with the 'abathochroal' eyes of *Pagetia* described by Jell (1975). *Shizhudiscus* is found at a lower horizon than *Neocobboldia*, in the Qiongzhusi Stage. The eyes of *Shizhudiscus* are the holochroal. They are the oldest known from China, they show clearly many primary characters, and indeed are amongst the most ancient trilobite eyes of all.

LOCALITIES AND STRATIGRAPHY

All specimens described in this paper came from two localities: Xichuan, Henan, and Pengshui, Sichuan (Text-fig. 1A). Since the former locality has been already described and the stratigraphy tabulated in detail (Zhang 1987), only a stratigraphical section (Text-fig. 2) for the latter is given here – the Longquanxi section, which is about 80 km north of Pengshui, in south-east Sichuan (Text-fig. 1B).

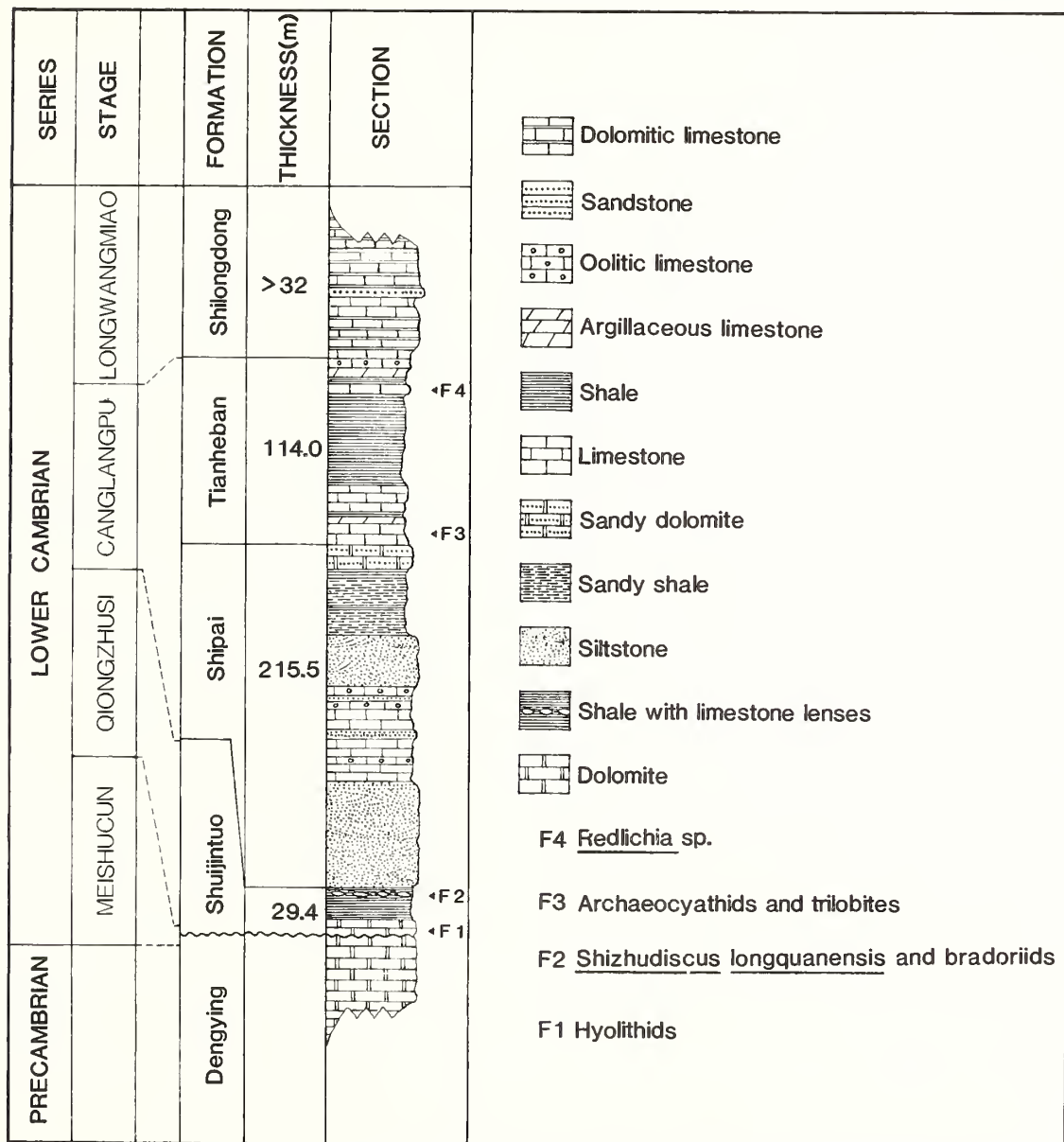
Shizhudiscus is widely distributed in China, and has been recorded from Shaanxi, Guizhou, and Xinjiang as well as from Pengshui, but is always associated with *Eoredlichia*, *Wutingaspis*, and *Zhenbaspis*. All of these have been regarded as of Early Cambrian (Qiongzhusi Stage) age (Lu *et al.* 1982), and this is clearly earlier than *Neocobboldia*. These genera appeared almost at the



TEXT-FIG. 1. Sketch map showing the location ('I') of the Longquanxi section at Pengshui, Sichuan, China, where all specimens of *Shizhudiscus longquanensis* S. G. Zhang and Zhu investigated in this study were collected.

beginning of the trilobite record in China, directly following a horizon of small shelly fossils. Although Brasier (1989) suggests that the base of the trilobite-bearing Cambrian in China is younger than in Morocco and North America, where olenelloids occur, the phosphatized eyes of *Shizhudiscus* that have been obtained are the earliest really well-preserved trilobite eyes so far known from anywhere in the world, and clearly represent a most important stage in their evolution.

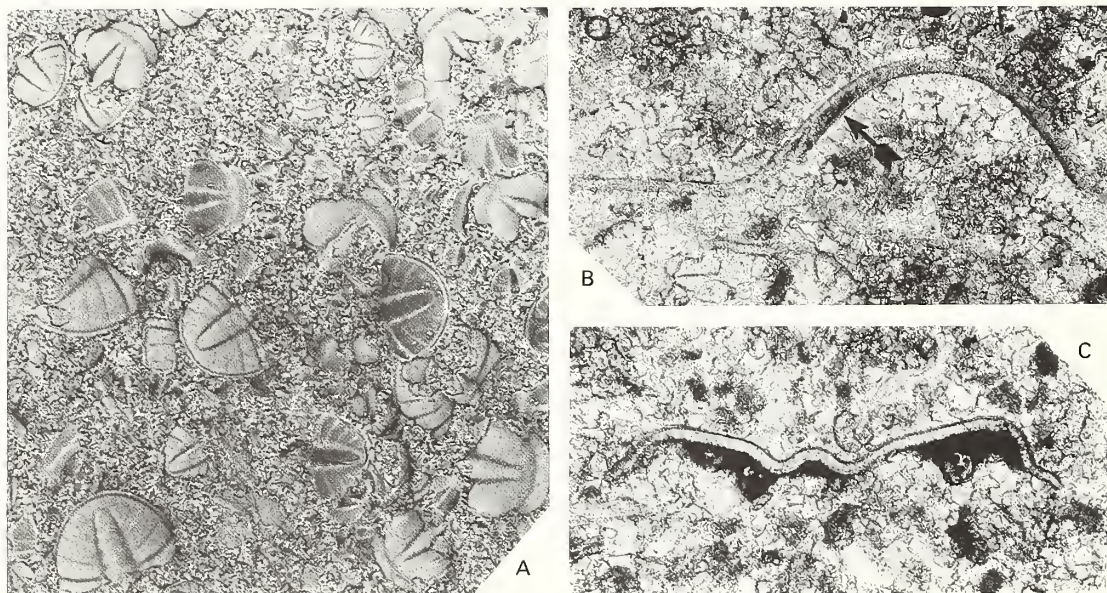
In the Longquanxi section there are about ten thin beds or flat lenses of limestone within black shale. Most of these limestones yield *Shizhudiscus*, but they obviously cover a certain time span. To avoid the possible influence of variation that might arise from a mixed population of individuals that lived at different times, only specimens that came from a single horizon were used in this study.



TEXT-FIG. 2. Columnar section through the Lower Cambrian at Longquanxi, Pengshui, Sichuan, China.

PRESERVATION

The Lower Cambrian trilobites discussed here, *Neocobboldia* and *Shizhudiscus*, have all been preserved by phosphatization and most of them have been extracted from the rock matrix by solution with 3–5 % acetic acid. It is very probable that the cuticle was originally composed mainly of calcium carbonate as is the case with other trilobites, but there may have been an additional primary phosphate component. The exuvia are preserved either by encrustation with secondary phosphate, or by replacement of the cuticle itself by phosphate; sometimes there may be both replacement and encrustation. These modes of preservation are evident in specimens dissolved out of the rock, but the extent of phosphatization in our material, even within the same sample is very variable. When a block whose surfaces are replete with trilobite exuvia (Text-fig. 3A) is dissolved in acid, the number of specimens actually recovered as three-dimensional objects may be many fewer than expected. This is because many specimens are hardly phosphatized at all, the others in varying degrees. Thin sections confirm that only some of the specimens have phosphate coats or patches of secondary phosphate within the cuticle. Whether, and to what extent an individual exuvium was preserved by encrustation depended upon a delicate balance of surface chemical conditions.



TEXT-FIG. 3. A, mode of occurrence of *Shizhudiscus* on bedding planes within concretions, Longquanxi section, Gr. I. 69317, $\times 9$. B, thin-section showing both phosphatized black rims on the trilobite cuticle, and invasion of cuticle by phosphate, Gr. I. 69318, $\times 85$. C, thin section showing phosphatized black rims on the cuticle and phosphatic overgrowth on lower surface, Gr. I. 69319, $\times 85$.

Preservation of Shizhudiscus. Where preservation by encrustation has taken place, the secondary phosphate always coats both the internal and external surfaces. What is visible from the outside therefore depends largely upon the relative thickness of the secondary phosphate cover. Where the phosphate is very thin and forms only a light coating on the outer surface, the surface of the eye with its convex lenses is more or less perfectly replicated by the thin phosphate film. Both the internal and the external surface may be preserved in this way. If the secondary phosphate coating is thicker, however, the lenses may be partially or totally obscured.

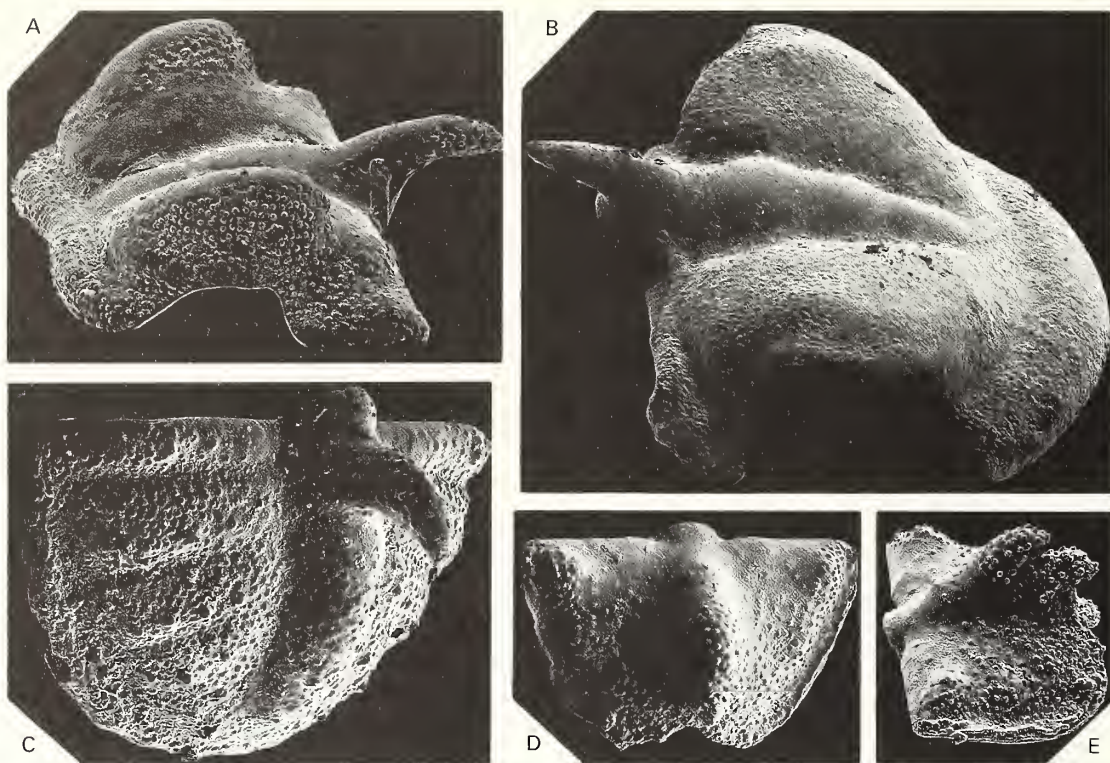
For most specimens of *Shizhudiscus* replacement is common, and specimens usually have both the outer and inner surfaces of the cuticle phosphatized, so that fine details of ornamentation on the outer surface of the carapace is exceptionally well preserved (Text-fig. 4A–E; Pl. 1, figs 8 and 9). This is quite different from that on the surface of the internal layer. In thin section the phosphate replacing both the outer and inner layers shows as a thin opaque film on both the outer and inner surfaces (Text-fig. 2B, C). It seems that the outermost and innermost cuticular layers are easily replaced by phosphate, since it has been found that in many specimens only these layers are altered, leaving the inner parts unchanged (Pl. 1, figs 2, 5, 6, 7). Although most cuticles seen in thin section normally show only black phosphatic rims, there are some instances in which the phosphate shows as a black amorphous mass invading the inner part of the cuticle itself (Text-fig. 3B). In such cases the main internal part of the cuticle could be preserved by replacement. While such phosphatization of the internal cuticle is less common, confirmatory evidence that it does happen comes from acid-etching. The application of a 10% aqueous solution of ethylenediaminetetracetic acid (disodium salt) to a polished surface of the rock lightly dissolves the carbonate matrix so that the phosphatized outer and inner layers stand up from the surface. While these phosphatic shells replacing the outer and inner surfaces of an individual specimen appear quite distinct, the occasional partial filling or presence of irregular phosphate bars connecting the two layers indicate that the cuticle itself has been phosphatized.

Some specimens, however, have a phosphate coating on their outer surface (Pl. 2, fig. 2), and it is not clear whether the cuticle below it is replaced or not. From a specimen (Pl. 2, fig. 1) directly examined in its rock matrix it is apparent that the outer layer of the eye, which has been partly flaked off, seems too thick to be considered as a single corneal surface. Its thickness may suggest the presence of a phosphate coating. It is of interest to note that this unusual preservation of the eye of *Shizhudiscus* is quite different from that of other known modes of preservation in trilobite eyes, for the inner surface of the lenses has been preserved as a continuous thin layer, running smoothly into the inner surface of the cuticle.

Because the outer layer of the lens is flatter than the inner layer, and the outer surface of the lens may be partially or totally obscured by a phosphate coating (Pl. 2, fig. 2), or to some extent irregular (Pl. 1, fig. 1a), most observations on lens number, morphology, arrangement, and ontogeny have been made with reference to internal moulds of the lentiferous surface.

Preservation of Neocobboldia. Only a few specimens of *Neocobboldia* have been preserved by phosphatic replacement of the cuticle, but these exhibit many details of fine structure on the outer surface (Pl. 3, fig. 1). Most specimens, however, were preserved by encrustation, and the secondary phosphate always coats both the internal and external surfaces. Unfortunately, we have obtained only a very few really small librigenae, and these are almost covered by a thick coating of phosphate. The smaller the specimens, the more thickly they tend to be covered, so that the early stages in ontogeny of the eye are less clear than would be desirable. If the external shell of secondary phosphate is removed, the inner surface of the lens array can be clearly seen as an internal mould (Pl. 3, fig. 8), and likewise the external mould of the surface is visible from the inside. On the whole, the replication of the visual surface as moulds is excellent, and can give near-perfect details of the lens surface, but this depends upon the relative completeness of phosphatization. This is apparent in the series of specimens of *Neocobboldia* illustrated on Plate 3, figures 3–5, which show different degrees of secondary phosphatization. In figure 3 only the proximal parts of the lens surfaces are well preserved, elsewhere the phosphate forms only a dense meshwork; in figure 4 it is more complete, though replication of the whole lens surface is still not quite perfect, whereas in figure 5, the surface of the lenses is an exact mould of the original. In such instances the true shape of the lenses can be appreciated; in the case of *Neocobboldia* they conform to the ideal model of a thick but aplanatic lens, as designed by Des Cartes in 1637 (Clarkson and Levi-Setti 1975).

The presence of so much diagenetic phosphate in these Lower Cambrian rocks is associated with a major global phosphogenic event around the Precambrian/Cambrian boundary (Cook and Shergold 1984). The highest concentrations of phosphate in rocks of this age are actually found in

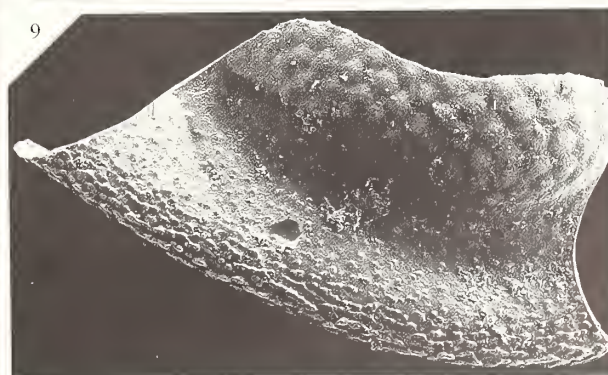
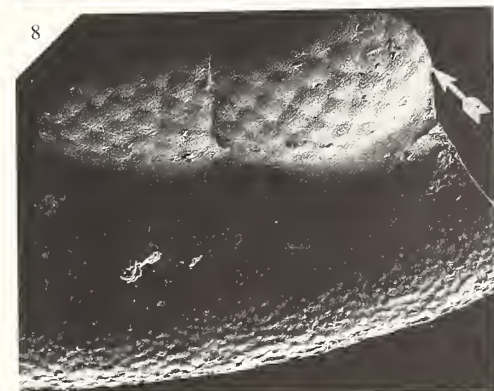
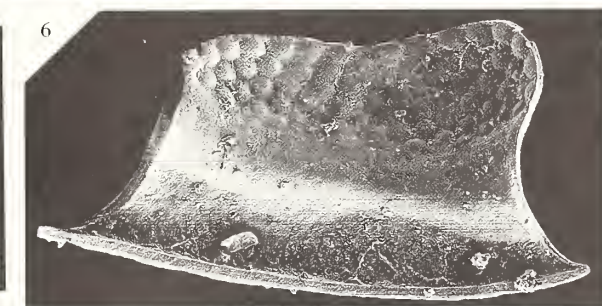
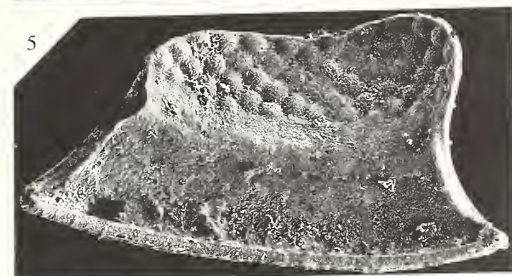
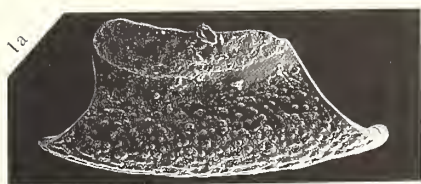


TEXT-FIG. 4. *Shizhudiscus longquanensis*. S. G. Zhang and Zhu, Lower Cambrian, Longquanxi, Pengshui. A, Gr. I. 69251, oblique lateral view of a protaspid cranium, $\times 128$. B, Gr. I. 69252, oblique lateral view of a holaspid cranium, showing outline of facial suture, $\times 70.5$. C, Gr. I. 69253, oblique lateral view of a meraspid pygidium, $\times 128$. D, E, Gr. I. 69254, protaspid pygidium; D, dorsal view; E, oblique lateral view, $\times 128$.

southeast Asia, whence our material comes, and Cook and Shergold refer specifically to the Lower Cambrian of southwestern China as one of the major phosphorite areas in the world. The presence of a rich and specialized Early Cambrian eodiscid fauna in southwestern China (Zhang *et al.* 1980) may be associated with very high productivity at this time. The abundance of phosphate was related by these authors to a period of enhanced oceanic overturn, following a long time period when such overturn was slight. This brought nutrients up into the photic zone, and whereas much of the

EXPLANATION OF PLATE I

Figs 1–9. *Shizhudiscus longquanensis* S. G. Zhang and Zhu, Lower Cambrian, Longquanxi, Sichuan. 1a, b, Gr. I. 69255; a, lateral view of smallest right librigena, $\times 123$; b, internal view of same specimen, showing nineteen lenses (including half-lenses) and their pattern of arrangement, partially eroded but still recognizable, $\times 410$. 2, Gr. I. 69256, internal view of a right librigena with twenty-two lenses, $\times 123$. 3, Gr. I. 69257, internal view of a right librigena with thirty-four lenses, $\times 123$. 4, Gr. I. 69258, internal view of a right librigena with forty-two lenses, $\times 123$. 5, Gr. I. 69259, internal view of a right librigena with fifty-one lenses, $\times 123$. 6, Gr. I. 69260, internal view of a right librigena with sixty-nine lenses, $\times 123$. 7, Gr. I. 69261, lateral view of the largest left librigena with ninety-six lenses, $\times 123$. 8, Gr. I. 69262, lateral view of a damaged left librigena showing a half-lens (arrowed) at the posterior margin of the eye. $\times 123$. 9, Gr. I. 69263, lateral view of a left librigena showing the regular arrangement of small lenses, $\times 123$.



phosphate so released was used up in animal and algal metabolism, and for building skeletons, some was made available for diagenesis. The type of preservation we see in the Chinese material is very similar to that noted by Jell (1975*a, b*) in small trilobites preserved during the somewhat later (Middle Cambrian) phosphate 'boom' in Australia.

In general terms, the high-concentration phosphorite episode, which was probably associated with major evolutionary changes at this time, and has allowed such superb preservation, was over long before the Upper Cambrian.

GEOMETRY OF THE VISUAL SURFACE IN TRILOBITES

Our material includes a gradational size series of eyes showing various stages in development for both *Shizhudiscus* and *Neocobboldia*. This has enabled us to work out how the visual surface grows and how the lenses were emplaced. While this is generally similar to that of other trilobite eyes there are some differences in detail, so a brief review of trilobite eye ontogeny and visual surface geometry is given here so that our new information on development of eodiscid eyes can be interpreted in terms of what is already known.

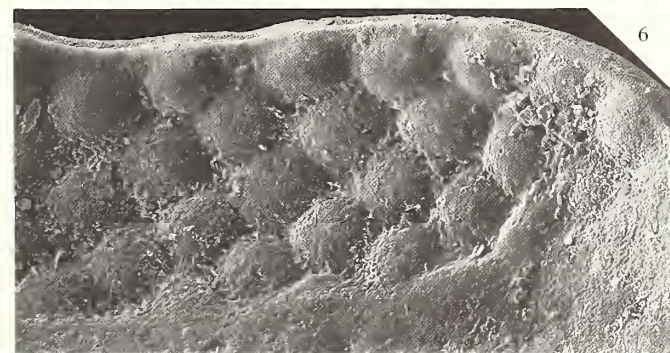
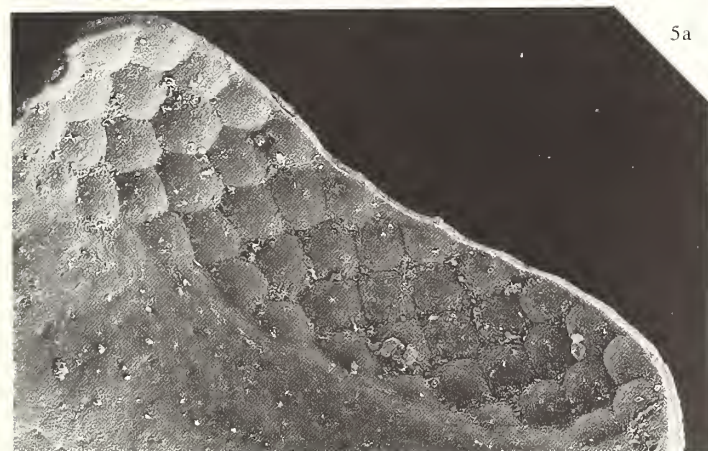
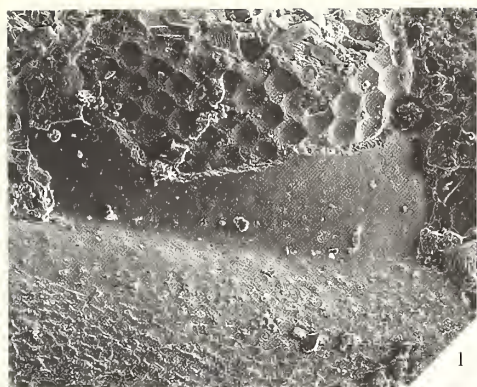
All trilobite eyes known at present, whether holochroal or schizochroal, grow in the same general way (Beckmann 1951; Clarkson 1971, 1975, 1979). They begin their growth as a thin strip of lens-generating cuticle, the generative zone, just below the palpebral lobe. The first horizontal row of lenses is produced from the generative zone which moves downward as the visual surface enlarges, so that new lenses are added at the base of the eye as the generative zone advances, and once produced are permanently 'frozen' into place.

The genetic programme governing the expansion of the visual surface (dominantly downward but also anteriorly and posteriorly) is independent of that governing the emplacement of the lenses, though the two are obviously related. When new space is made at the base of the eye by the generative zone new lenses are formed upon it, but their emplacement follows a defined programme so that they are normally fixed to the bottom of pre-existing files and they will grow until the proximity of neighbouring lenses prevents their further expansion.

In nearly all cases the resultant pattern is a hexagonal close packing system but there are many different versions of this, some involving a change of lens size over the visual surface. Such patterns, many of which have been analyzed in detail (Clarkson 1975) are different answers to the problem of packing lenses in a regular pattern from a single marginal generative zone onto a curving visual surface (Clarkson 1979, p. 6). This is a fundamental problem for the growth of all trilobite eyes including those of the eodiscids, which, while conforming generally to the normal growth patterns, exhibit some striking peculiarities all of their own.

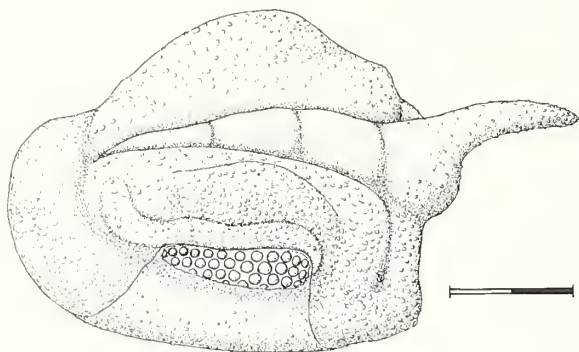
EXPLANATION OF PLATE 2

Figs 1–8. *Shizhudiscus longquanensis* S. G. Zhang and Zhu. Lower Cambrian, Longquanxi, Pengshui. 1, Gr. I. 69264, a librigena within the rock matrix, showing internal moulds of small lenses and partial preservation of their outer surfaces, probably the result of encrustation by secondary phosphate, $\times 128$. 2, Gr. I. 69265, an isolated librigena, showing internal mould of small lenses and secondary phosphate on the outer surface, $\times 176$. 3, Gr. I. 69266, internal view of a right librigena, showing large lenses, $\times 324$. 4, Gr. I. 69267, oblique internal view of a broken eye, showing the inner (black arrowed), and outer (white arrowed) layers of small lenses, $\times 400$. 5*a, b*, Gr. I. 69268; *a*, internal view of a left librigena showing the irregular size and arrangement of the small lenses and the sensory pits below the eye, $\times 272$; *b*, detail of the same eye, showing the two layers of lenses, the separate rounded lenses of the upper row, the polygonal lenses in the centre of the eye, and half-lenses along the lower edge, $\times 680$. 6, Gr. I. 69269, internal view of a left librigena, showing half-lenses along the lower margin of the eye, unequally developed, $\times 400$. 7, Gr. I. 69270, internal view of a right librigena, showing half lenses towards the anterior of the eye, $\times 400$.



MORPHOLOGY AND GROWTH OF THE EYE IN *SHIZHUDISCUS*

Many librigenae of *Shizhudiscus* were available for this study. Unfortunately none of these are preserved in their original position, attached to the cranidium. The cranidium, however, clearly shows the outline of the facial suture, which slopes anteriorly at about 45° , is nearly flat below the palpebral lobe, and descends steeply posteriorly. This constant shape enables isolated librigenae that are bounded by the facial suture to be identified as belonging to the left- or right-hand side of the trilobite (Text-fig. 5). In addition, variation in size of these librigenae indicates that they represent different growth stages. The smallest we have, according to its size and outline, may have separated from a cranidium of late meraspid or early holaspid stage, while some of the larger ones can undoubtedly be referred to the adult stage.

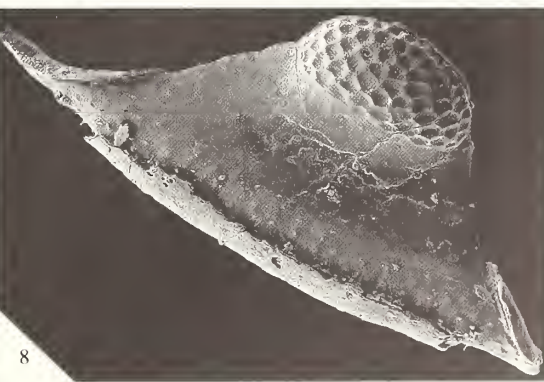
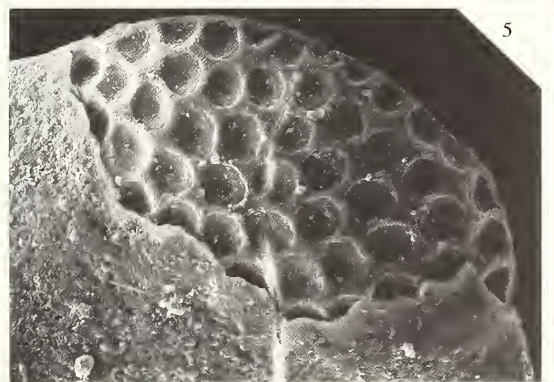
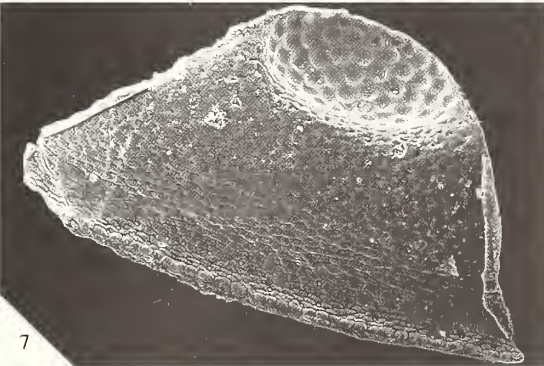
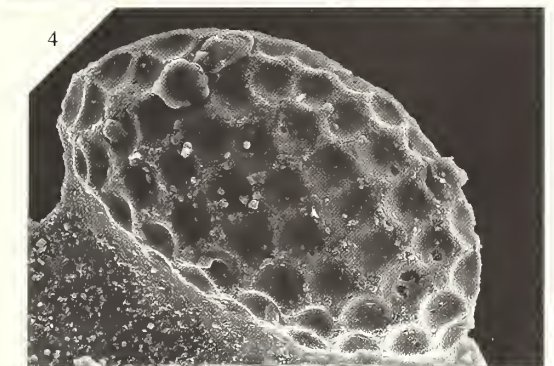
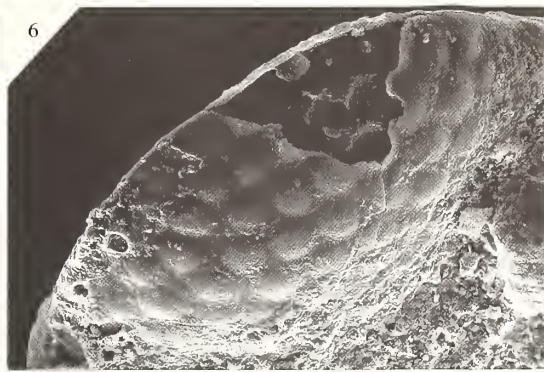
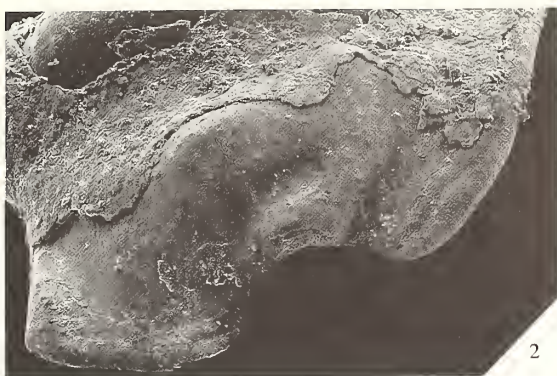


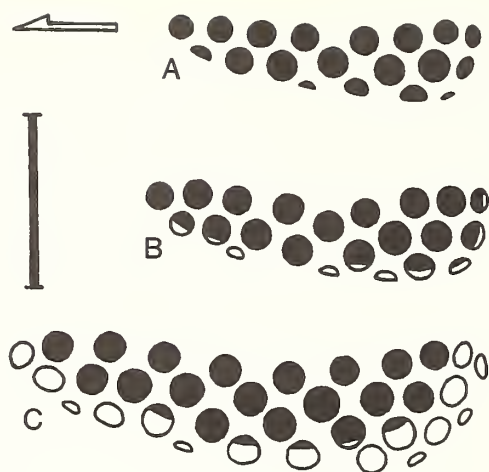
TEXT-FIG. 5. Reconstruction of an early holaspid cephalon of *Shizhudiscus longquanensis* S. G. Zhang and Zhu in oblique-lateral view, showing the left librigena in its original position. Scale bar = 0.2 mm.

The eye of *Shizhudiscus* forms a relatively narrow, elongated band with subparallel upper and lower surfaces, somewhat higher at the rear. It is set at the summit of the librigena, which is about twice the height of the eye itself. The lenses are contiguous and are usually of polygonal form. It has been observed that as the eye grows, it stays much the same shape, always retaining an elongated kidney-shaped outline. Some general principles of growth are evident. Firstly, it is readily seen that as the librigenae increase progressively in size, so the lenses gradually become larger. For some small librigenae, the average lens diameter ranges from 19–25 μm and for some of the largest ones the range is from 30–45 μm . Secondly, the smaller the specimen, the fewer the lenses it bears. A comparison of the different growth stages represented in the series shows how the lenses are emplaced (Text-fig. 6).

EXPLANATION OF PLATE 3

Figs 1–8. *Neocobboldia chinlinica* Lee. Lower Cambrian, Xichuan, Henan. 1, Gr. I. 69300, oblique lateral view of a meraspid cranidium with minutely ornamented outer layer, showing the arched palpebral suture, $\times 104$. 2, Gr. I. 69301, oblique dorsal view of a holaspid cranidium, showing the arched palpebral suture, $\times 105$. 3, Gr. I. 69302, poor phosphatization of eye, $\times 264$. 4, Gr. I. 69303, incomplete phosphatization of eye, $\times 271$. 5, Gr. I. 69304, perfect phosphatization of eye, $\times 268$. 6, Gr. I. 69305, outer surface of somewhat damaged eye, coated with very thin phosphate and showing separated rounded lenses, also well-preserved internal mould below the flaked-off outer surface, $\times 268$. 7, Gr. I. 69306, external mould of a right librigena, showing the smooth outer surface of the rounded lenses, and minutely ornamented librigena, $\times 112$. 8, Gr. I. 69307, a left librigena with the outer layer and phosphatic coating flaked off; the irregular polygonal packing of the lenses on the internal mould is due to erosion of the originally separated lenses, $\times 104$.





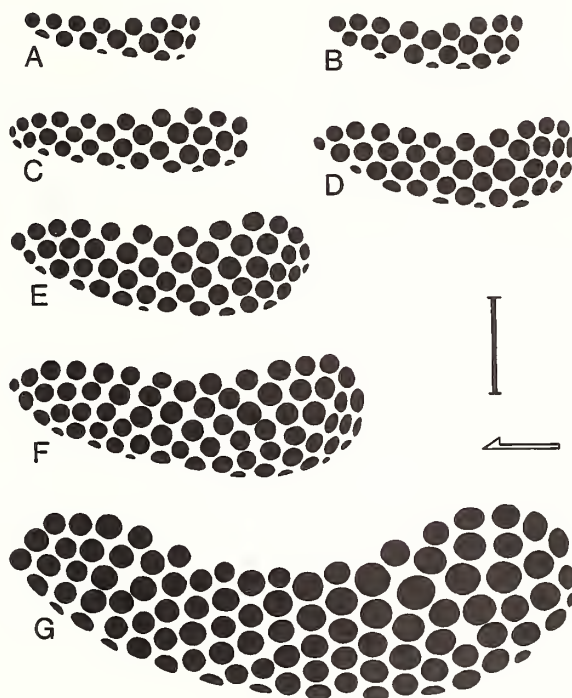
TEXT-FIG. 6. Schematic diagram of early growth stages of the eye of *Shizhudiscus longquanensis* S. G. Zhang and Zhu. A, the smallest librigena with nineteen lenses (including about six half-lenses). B, a somewhat larger librigena with twenty-two lenses: the filled circles or part circles correspond to the lenses or half-lenses in librigena A; the blank parts represent the increase of lenses with growth. C, a still larger librigena with thirty-four lenses, showing lenses or half-lenses corresponding to B (filled circles or part-circles), and the increase in number of lenses with growth; the arrow indicates the anterior. Scale bar = 0.2 mm. See also Text-fig. 7.

The earliest stage in the development of the visual surface must have been the emplacement of a single horizontal row of five or six lenses directly below the palpebral suture. In our smallest specimen, though the phosphate coating is lumpy and irregular so obscuring the details, nineteen lenses (including half-lenses) can be recognized, of which the middle ones are separated laterally from each other by small gaps. These lenses and gaps remain a constant feature throughout the subsequent development of the eye, and can be used as a reference point for tracing the fate of individual lenses. Following the emplacement of the upper horizontal row a second horizontal row is then laid down below it, each of the lenses set between and below the lenses of the upper horizontal row, with the vertical and lateral spacing of the lens centres being about the same. At this stage the upper margin of the eye, along the palpebral suture is virtually flat. As the eye grows, further rows of lenses are added below in regular sequence, but at the same time the eye expands laterally both at the front and the rear. The gradational size series of specimens allows the mode of addition of extra lenses to be established. For while the visual surface is expanding downwards, the upper horizontal row receives new lenses both anteriorly and posteriorly, thus extending itself in both directions, though curving downwards to follow the contour of the facial suture. The upper horizontal row thus retains its apparent identity, though it has grown by accretion in both directions away from the centre.

The lenses that lie along the lower margin of the eye are truncated by the margin of the visual surface so that they appear as semicircular half-lenses. Such half-lenses can sometimes be found also at the posterior (Pl. 1, fig. 8) or anterior (Pl. 2, fig. 8) edges. It has been observed that such half lenses are present in varying degree on every librigena (Pl. 2, figs 3, 5, 7). We consider these to be immature, which implies that, as in other trilobites, the generative zone lies along the anterior, lower, and posterior edges of the eye, and that lenses were emplaced along this generative zone as the eye grew. Two alternative models for growth may be considered. The first is that a single lens could only be fully formed after two moult stages. If this were so, then it may be presumed that the genetic programme responsible for producing new lenses along this margin went into action before each moult. While new, soft cuticle was being formed prior to ecdysis, a number of new lenses and associated visual units below were developing along the lower margin of the eye. The timing of ecdysis was controlled by an over-riding and different programme, which operated when these marginal lenses were imperfectly formed, as represented by the 'half-lens' stage. At the first moult, therefore, they were not fully functional; they only became so after the next moult, by which time they were round and probably were fully functional. The second possibility is that the genetic programme for lens-development was independent of ecdysis so that new lenses continually appeared along the lower margin of the visual surface at any time during growth. This is very

unlikely, however, since the visual surface is shed as a whole unit, and the hardness of the cuticle would inhibit the eruption of new lenses. A zone of half-lenses on the lower margin of the eye is characteristic not only of *Shizhudiscus* but also of *Neocobboldia* and the two specimens of *Pagetia* figured by Jell (1975, fig. 36D). It is not known from other trilobite eyes and seems to be a feature unique to the eodiscids.

TEXT-FIG. 7. Schematic diagram of growth stages of the eyes of *Shizhudiscus longquanensis* S. G. Zhang and Zhu, showing increase in size and number of lenses and expansion of the visual surface with growth. The regular arrangement of the lenses in curving files or rows can be recognized, but irregularities become more pronounced with growth. The arrow indicates the anterior. Scale bar = 0.2 mm.



Over most of the eye the system of lens packing is more-or-less regular, and approximates a pattern of cubic close packing (Text-fig. 7). In such a packing system the lens-centres are equidistant from one another, so that the immediately evident appearance is of two intersecting diagonal rows inclined at 45° to the horizontal but at 90° to each other. The vertical files which form the third intersecting set consist of more widely spaced lenses and are harder to recognize. Cubic close packing is not common in trilobites. Hexagonal close packing on the other hand is normal: it is a more economical system which allows better use of the available space, and the accommodation of relatively more lenses per unit area. The only other recorded example of cubic packing is in the schizochroal-eyed *Phacops turco* aff. *praecedens* Haas, from the Eifelian of Morocco, discussed by Fortey and Morris (1977), which represents a departure from the normal phacopid packing. It is interesting, however, that cubic close packing is found in the eodiscids, which bear the earliest known well-preserved eyes. A cubic system, in which all lens-centres are equidistant is easy to generate. It can be done by a somewhat simpler genetic developmental programme than a hexagonal close packing system. Might this be the reason for cubic packing in the Lower Cambrian? Although the cubic packing system is recognizable, it is never absolutely regular; the vertical files are often sinuous and in places extra lenses seem to be intercalated. Moreover the lenses are larger and less regularly spaced posteriorly, which we interpret as a consequence of developmental constraints imposed by the shape of the visual surface. This must have been controlled by a separate genetic programme to that governing lens-emplacement, and the irregularities seen have developed because the separate genetic 'blueprints' had slightly conflicting instructions.

Anteriorly the facial suture curves downwards fairly gently, whereas at the rear it swings much more sharply downwards in a semicircular curve. It seems that the shape of the facial suture at this point is the primary determinant of the geometry of lens packing towards the rear of the eye, for it imposes a constraint on the number and arrangement of the lenses that can be packed in below it. There is only a limited amount of space in the expanding area enclosed beneath the downwardly curving upper horizontal row, though the curvature of the visual surface in this region, as seen in plan, is higher here than in any other part of the eye, and this allows more room for the lenses that are present to grow. While the regularity of spacing of lens centres breaks down to some extent, these same centres are more widely spaced than in other parts of the eye, and the lenses make use of the available space to grow larger (Pl. 2, figs 3 and 5). The rather unusual lens arrangement is based first on the cubic close packing system, with its 45° inclination of the diagonal rows, rather than the more usual 30° inclination, and secondly on irregularities in the posterior part, mainly determined by geometrical constraints consequent on the form of the facial suture. The later stages in the growth of the eye are illustrated in Text-figure 7. When the maximum depth of the visual surface has been achieved, usually after three or four horizontal rows have been emplaced, the eye still expands laterally, and the final lenses are added at the lower anterior and lower posterior margins. The development of the eye, as in other trilobites, must have operated upon a genetically controlled rolling programme basis. The largest eyes of all still have half-lenses along the base of the eye; presumably these were 'frozen' before their full development had been completed. This happened at each moult stage, and may also have been the case when the trilobite was fully grown, and when the genetic programme which finally ended the development of the eye came into operation.

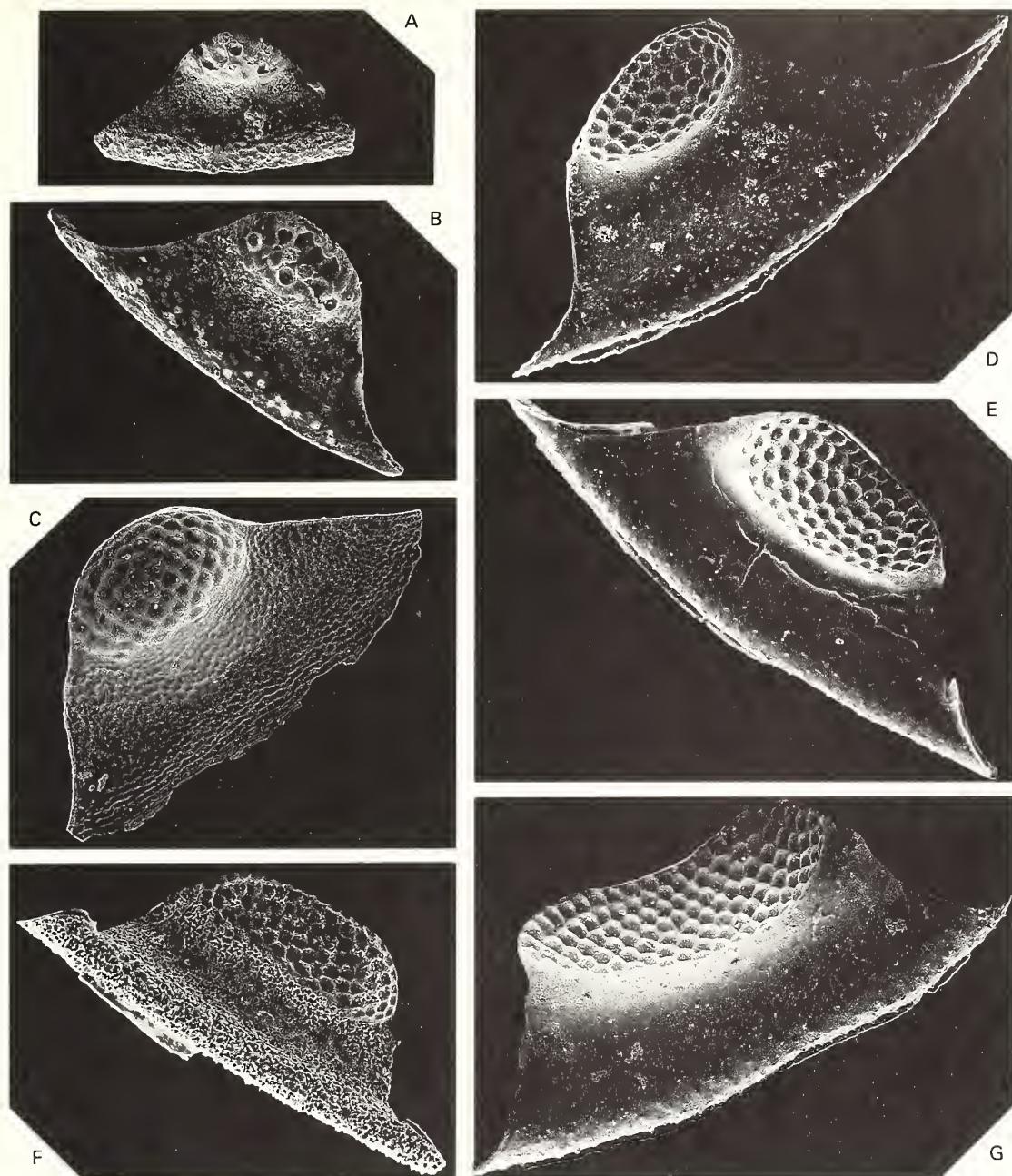
Although it has not proved possible to measure the angular range of vision in so small an eye as that of *Shizhudiscus* nor to make an accurate stereogram of its visual field (cf. Clarkson 1966a, b, 1975), an eye such as this has a horizontal range of about 70°, the fields of the two eyes not quite meeting at front and rear, and a latitudinal range from just below the equator to about 30° above the sea floor.

MORPHOLOGY AND GROWTH OF THE EYE IN *NEOCOBOLDIA*

The abundant phosphatized material of *Neocobboldia chinlinica* Lee, from Xichuan, Henan, has enabled all stages in the ontogeny to be worked out in detail and statistically processed (Zhang 1989). The smallest librigena we have (Text-fig. 8A), according to its size and outline, corresponds to a cranidium that has been assigned to an early holaspide stage. The specimens are preserved mainly by phosphatic encrustation and details of structure are normally best established by studying internal and external moulds. In some instances, where the phosphate forms a very thin film or in rare instances of replacement, the external morphology of the visual surface is easily appreciated.

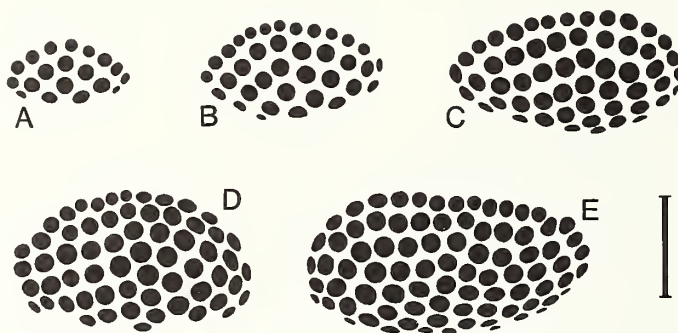
In specimens of average size the eye is an oval body, the dorsal edge of which, bounded by the palpebral suture, is the more strongly curved. Such eyes have about fifty lenses, though some very large specimens, in which the palpebral suture is flatter, may have up to eighty (Text-fig. 8E). The lenses are arranged in a packing system, analyzed below, which is semi-regular. There are three respects in which the eye of *Neocobboldia* differs from that of *Shizhudiscus*:

1. The palpebral suture forms an arch rather than a horizontal line (Pl. 3, figs 1 and 2); a factor which imposes certain constraints upon the geometry of the visual surface.
2. The lenses are separated one from another, as is clear both from the outer surface and the internal mould. The eye is thus like that described by Jell (1975) in the eodiscid *Pagetia oculata* as 'abathochroal'.
3. The proximal surface of each lens, in well preserved specimens, has a centrally placed nipple, marked on the internal mould by a corresponding dimple (Pl. 4, figs 3 and 6a, b). Such a lens is similar in form to the ideal thick, but aplanatic lenses designed by Des Cartes in 1637, and detected in the Ordovician phacopid *Dalmanitina* (Clarkson and Levi-Setti, 1975). The latter genus, however, has an additional structure, the intralensar bowl, which in *Neocobboldia* seems to be lacking.



TEXT-FIG. 8. A-E, a series of librigenae of *Neocobboldia chinlinica* Lee, probably representing different holaspide growth stages. Lower Cambrian, Xichuan, Henan; A, Gr. I. 69308, a left librigena with nineteen lenses (including half-lenses); B, Gr. I. 60309, a left librigena with thirty-six lenses, outer surface partially preserved; C, Gr. I. 69310, an external surface of a left librigena with fifty-five lenses; D, Gr. I. 69311, internal mould of a right librigena with sixty-two lenses; E, Gr. I. 69312, an internal mould of a right librigena with eighty-four lenses; the outline of the eye has changed to elongate ovoid. F, G, two librigenae of an unknown genus; F, Gr. I. 69400, a librigena with an elongate eye, composed of eighty-three small lenses in close contact; G, Gr. I. 69401, a larger eye with many small lenses. All $\times 112$.

The visual surface seems to be separable into three zones: an upper row, a central semi-regular zone, and a basal zone of half-lenses. It is possible, by studying individual growth stages, to work out how the lenses were emplaced as the eye grew, but because lens-packing is quite variable from one eye to another (Text-fig. 9), this imposes some limits on interpretation.

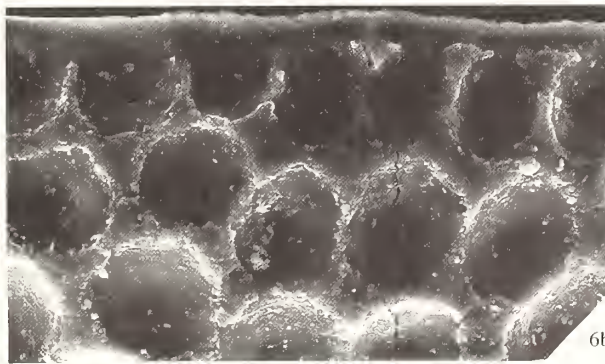
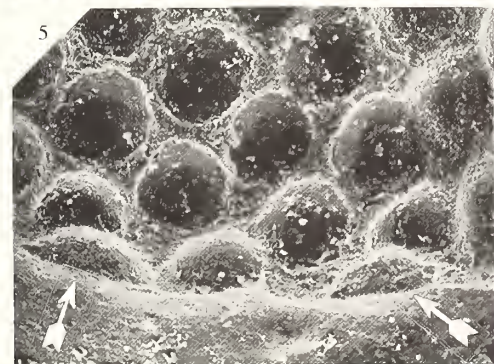
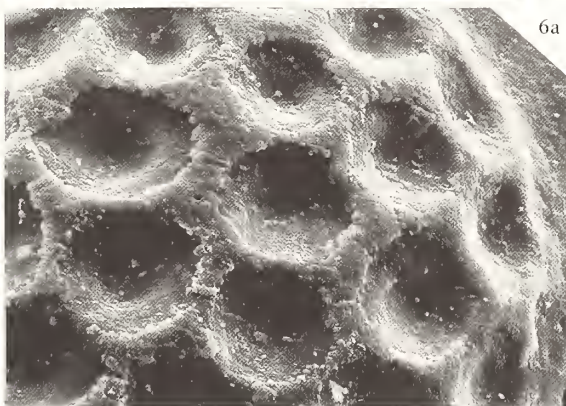
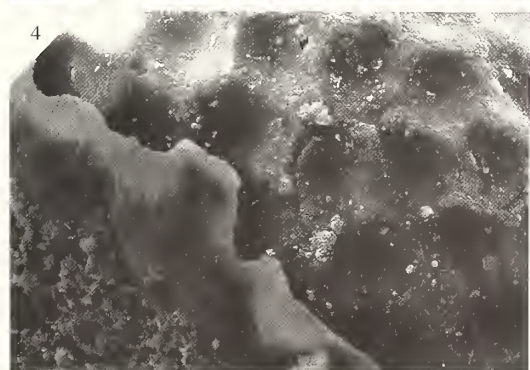
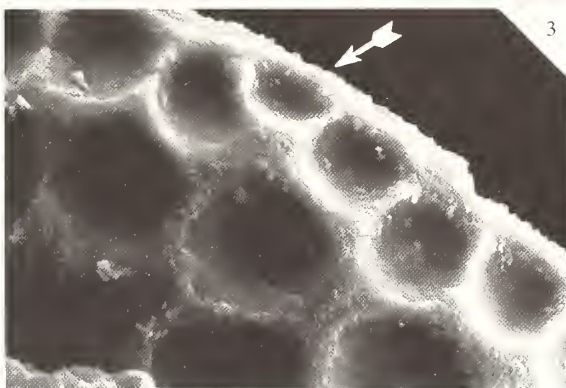
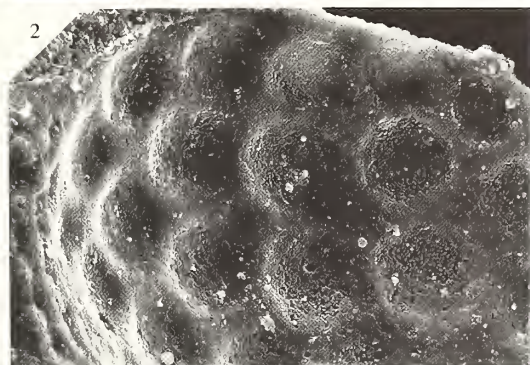
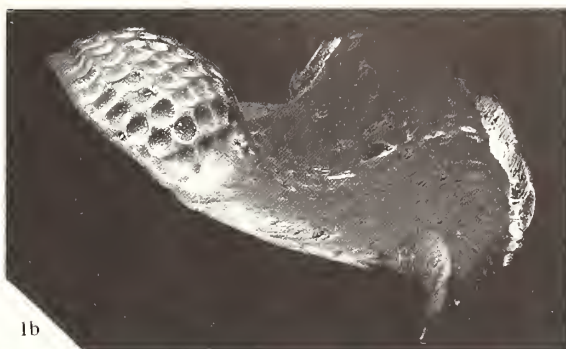
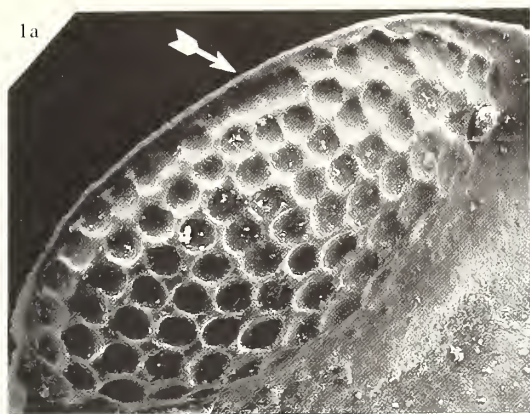


TEXT-FIG. 9. Schematic diagram showing growth stages of the holaspid eye of *Neocobboldia chinlinica* Lee, exhibiting the irregular arrangement of small lenses and change in the outline of the eyes. A, B, E, left eyes. C, D, right eyes. Scale bar = 0.2 mm.

The upper row, lying just below the palpebral suture and equivalent to the upper horizontal row of other trilobite eyes, consists of an arched string of lenses. The central three or four lenses of this chain are usually much smaller than the others of the same row (e.g. Pl. 3, figs 5 and 7; Pl. 4, figs 3 and 6b); they are here termed the 'initial set'. Sometimes the upper margin of these lenses is truncated so that they form half-lenses. In many cases this initial set of lenses is separated by a sharp discontinuity in size or level from the neighbouring lenses, anteriorly, posteriorly, or indeed in both directions. In rare instances, the lenses of this initial set are fused together (Pl. 4, fig. 1a) as if they had not separated properly during development. The initial set must represent the lenses which formed first, at a larval stage earlier than any represented in our material (our smallest specimens have about twenty lenses). It is clear, both from our gradational size series, and from the morphology of the adult eye, that new lenses were added both to the front and rear of the initial set, so that as the visual surface grew downwards, it also expanded anteriorly and posteriorly, more or less symmetrically, by addition of new lenses below the curving palpebral suture. The upper row in the adult eye has lenses increasing in size in both directions from the centre, and especially where the initial set is well marked, is clearly defined and thus seems rather distinct from the less regular lens-rows below.

EXPLANATION OF PLATE 4

Figs 1-6. *Neocobboldia chinlinica* Lee. Lower Cambrian, Xichuan, Henan. 1a, b, Gr. I. 69313, internal mould of a left librigena; a, showing the rounded lenses, and the 'fusing' of some of the lenses (including the 'initial set'; arrowed), of the upper horizontal row, $\times 254$; b, anterior view, showing the lenses arranged upon a moderately curved spherical surface, $\times 170$. 2, Gr. I. 69306, detail of an external surface, showing rounded, separate lenses, which seem to be covered by a common cornea, $\times 560$. 3, Gr. I. 69314, several small lenses of the 'initial set' (including arrowed lens and adjacent lenses to the right), located in the middle of the upper horizontal row, $\times 880$. 4, Gr. I. 69315, fine annular groove surrounding each lens, on phosphatized internal mould, $\times 560$. 5, Gr. I. 69316, imperfectly developed half-lenses (arrowed) truncated by later half-lenses of the basal zone, $\times 625$. 6a, b, Gr. I. 69312, well-preserved internal mould; a, showing centrally placed dimple for each lens, $\times 750$; b, showing small lenses of the 'initial set' in the middle of the upper horizontal row, $\times 750$.



Under the upper row is a broad, convex zone in which the lenses are arranged in more complex patterns, which vary quite markedly between one eye and another. Perhaps the most immediately evident features are second, third, and other rows, roughly concentric with the upper row, but intercalated lenses usually break down the regularity of arrangement in the lower parts of the eye. The lenses of the second row are usually of more uniform size than those of the upper row, emphasising the apparent difference between the two. Such concentric rows, however, form part of a hexagonal close packing system, which though not fully regular is still fairly well defined, and which seems to have begun to operate automatically, after the formation of the initial set. It is important to note that the visual surface retains its ovoid shape throughout development (at least until the latest stages when it has about eighty lenses and acquires a more elongate form). Thus concentric 'fronts' or zones of growth spread away from the initial set and adjacent lenses, though the variability of the eye of this species makes it difficult to establish the fate of individual lenses by direct comparison.

All the specimens, representing the various growth stages, have a zone of half-lenses along the downwardly bowed lower margin of the visual surface (Pl. 3, figs 3–8; Pl. 4, figs 1*a* and 5), equivalent to those of *Shizhudiscus*, and formed in the same way. There are some examples where lenses towards the base of the eye have themselves been truncated by later lenses. Plate 4, figure 5 clearly shows otherwise rounded lenses with their lower edges overprinted by the last, semicircular, lenses to be formed. Presumably the developmental programme which terminated the growth of the visual surface was not fully synchronized with the programme for lens emplacement; the latter continued for a time after the growth of the visual surface had stopped.

The irregularities which are so evident in all examples studied are of two kinds: those which arise as a normal consequence of packing lenses of fairly uniform size on a visual surface of this shape and those which seem to be abnormal. 'Normal' growth irregularities are widespread in the eyes of trilobites, and arise because of conflicting requirements of different programmes which govern growth (Clarkson 1975, 1979). A more evident malformation, however, is seen in Plate 4, figure 1*a*. This is an example of an eye in which the lenses of the initial set are not properly separated, and this imperfect separation extends some way anteriorly along the upper row. But it is posteriorly from the initial set that the lenses become more haphazardly packed, the irregularity affecting the posterior part of the upper row and also the lenses below it. It is quite probable that this abnormal arrangement may relate to the initial malformation.

In a very few particularly well-preserved specimens a fine annular groove is visible on the phosphatized internal mould of the visual surface surrounding each of the lenses (Pl. 4, fig. 4). These thin rings are preserved on the inner surface of the eye only, and probably represent the site of attachment of sublensar units, presumably of cylindrical form. If this is so, the interior of the eye may well have possessed a series of short, cylindrical capsules, one attached below each lens, as has been envisaged for the schizochroal eyes of *Phacopina*. Perhaps, then the eye is less 'abathochroal' (as envisaged by Jell (1975), whose model suggests that the cornea was anchored at the margin of each lens, on the upper surface) than 'schizochroal' and more similar to the eyes of *Phacopina*.

As with *Shizhudiscus*, the small size of the eyes of *Neocobboldia* precludes accurate measurement of the angular range of vision. Yet, in profile, the eye is much more highly curved (Pl. 4, fig. 1*b*), and subtended a latitudinal range of over 90° from the animal's equator to the pole. The longitudinal range as in *Shizhudiscus* was above 70° for each eye.

THE ROLE OF PAEDOMORPHOSIS AS AN EVOLUTIONARY CONTROL

Heterochrony, that is 'the change through time in the appearance, cessation, or rate of development of ancestral characters' (McNamara 1988), is increasingly recognized as a frequent and important control of trilobite evolution, from Lower Cambrian times onwards. Both paedomorphosis, and more rarely, peramorphosis have been demonstrated. Paedomorphosis (the retention of the juvenile characters of the ancestor as adult characters of the descendant) has recently been reviewed by

McNamara (1986, 1988), who noted three different categories of paedomorphosis and showed how their separate effects enable them to be distinguished.

The eye complex in trilobites was subject to paedomorphic changes and in particular to alteration by neoteny, a reduced rate of development of particular characters relative to that of the rest of the trilobite. Two such examples of neoteny have so far been demonstrated affecting the eye. The first is the retention of the visual surface by the librigena in some leptoplastine olenids as a derived condition (this is a juvenile feature of *Olenus* and allied genera which becomes fairly common in the later leptoplastines: see Clarkson 1973). Secondly, there is the origin of the schizochroal eye from a holochroal ancestral type. It is known that the meraspid eyes of *Paladin* have comparatively few round lenses, large with respect to the visual surface and separated from each other by intralensar sclera. Although this meraspid eye is like a miniature schizochroal eye, this aspect of its morphology is lost in the adult, where the lenses become closely appressed, and the eye becomes holochroal. It is from the juvenile condition that the schizochroal eye is considered to have been derived (Clarkson 1975, 1979).

The process of neoteny, so widespread in the history of the trilobites, may be invoked to account for the differences between the eye of *Shizhudiscus* and the closely related *Neocobboldia*. The eye of *Shizhudiscus* seems to be holochroal and has fairly thin biconvex lenses, all in contact, except for the central ones of the upper horizontal row, and of polygonal form. In contrast, the lenses of *Neocobboldia* are generally rounded and separate. The *Shizhudiscus* eye is here regarded as the 'ancestral' adult holochroal type. That of *Neocobboldia*, however, is interpreted as derived from the juvenile eye of a precursor, whose adult eye was of normal holochroal type, more like that of *Shizhudiscus*. In other words, the process is directly analogous to the envisaged derivation of the schizochroal eyes of phacopid trilobites, though with a lesser degree of specialization. It would be desirable to have confirmation of this from the juvenile eye of *Shizhudiscus*, but the early stages are normally too thickly encrusted by phosphate to allow the relative contiguity of the lenses to be seen. It is clear, however, that the first-formed lenses of the eye of *Shizhudiscus* in the centre of the upper row and the second row are separated one from another; which suggests that in the earliest stages of development the lenses were not in contact.

If it is correct to assume a neotenic origin for the eyes of *Neocobboldia* (and implicitly for the similar 'abathochroal' eyes of *Pagetia* and *Opsidiscus* described by Jell (1975)), it is of particular interest that the lenses conform to an idealized aplanatic Des Cartes model, in which the lower surface of each lens has a central nipple, as do the upper units of the lenses of the early schizochroal eyes of the Ordovician *Dalmanitina*, likewise believed to have risen by neoteny (Clarkson and Levi-Setti 1975). Possibly a similar larval lens structure may have become neotenuously modified in the same way; this is a rather critical area where more evidence may be sought in the future.

COMPARISONS WITH MODERN COMPOUND EYES

Compound eyes in present-day insects and crustaceans consist of radial bundles of cylindrical visual units, the ommatidia. Each of these is capped by a lens, beneath which is a crystalline cone, the main dioptric element. Under the crystalline cone, though not always in contact with it, is the photoreceptive element, or rhabdom. Nerves from the individual rhabdoms link with a large optical ganglion, lying below the ommatidia, in which the overall mosaic image is processed and enhanced.

Exner (1891) proposed that there were two distinct kinds of compound eye, known as apposition and superposition eyes. In apposition eyes the rhabdom is directly connected with the base of the crystalline cone. Each ommatidium is optically isolated from its neighbours and receives light through its individual lens only. These eyes, which are normal in diurnal organisms (and amongst marine crustaceans typical of brachyuran crabs, decapod larvae, and some amphipods and stomatopods) have good resolution, though photon capture is low and the image they form is not very bright. The lenses of apposition eyes are round or polygonal.

Superposition eyes have short spindle-shaped rhabdoms, each set towards the base of its ommatidium, and separated from the lower end of the crystalline cone by a clear zone. In these, light

coming through several adjacent lenses can be focussed on a single rhabdom, and a combined single image is formed at the level of the photoreceptors. Though this image is bright, it is poorly resolved by comparison with that of apposition eyes. Such eyes are characteristic of dark-adapted animals, and visual brightness is achieved at the expense of acuity. In bright light the individual rhabdoms can be isolated from each other by pigment which migrates along the length of the ommatidium to form a sleeve, so that the visual system can also function as an apposition eye.

Superposition eyes could not function unless the dioptric apparatus were able to bend the light rays more strongly than is normal between two media of different refractive index. Since this cannot be achieved by normal refraction, some kind of supplementary dioptric apparatus is needed. It is here that there may be some prospect of useful comparison with trilobite eyes, for the operation of these dioptric elements in crustaceans is directly related to the shapes of the lenses. Three kinds of superposition eyes have now been recognized in crustaceans:

1. *Superposition refracting eyes*. In these eyes, which are typical of mysids and euphausiids, and also of insects, the crystalline cone is a 'lens cylinder' (Exner 1891), in which the refractive index is graded, highest along the axis and lowest along the margins. This system permits light to be bent to a much higher degree than if the crystalline cone had been homogeneous. The cones are circular in cross-section, and the lenses round or hexagonal.

2. *Superposition reflecting eyes*. These eyes are found only in macruran decapods (lobsters, shrimps, etc.). The crystalline cones are 'square-sided plugs of jelly' (Vogt 1975; Land 1976). These act as orthogonal mirrors, and light reflects from their surfaces at twice its incident angle to produce an upright image at the level of the photoreceptor. Land has described them as acting optically as a 'silvered four-sided prism'. These dioptric elements work entirely by mirror-box reflection at their surfaces. They have to be square in cross-section to operate, and eyes of this kind are invariably distinguished by having square lenses.

3. *Superposition parabolic eyes*. Eyes of this kind have recently been described from portunid crabs (Nilsson 1988). They have inwardly-curved parabolic crystalline cones, round or square in cross section. They could easily have originated from apposition eyes.

Recognizing that there are several kinds of modern compound eyes, which can in some respects be distinguished by the shapes of the lenses as seen externally, is there any basis for comparison with eodiscids, or indeed with other holochroal-eyed trilobites? One's first impression might be that if the holochroal eyes of trilobites can be considered as at all similar to those of recent crustaceans, they are likely to have been of apposition type; this is because apposition eyes are the basic type from which various pathways led to superposition eyes of various kinds. The real problem in interpreting them further is that we do not know if the eyes of any trilobites had crystalline cones below the lenses. In crustaceans the cones form the main part of the dioptric system; in trilobites the whole optical function may well have been performed by the lens array alone. If there were cones our interpretation of how the eyes of trilobites worked is likely to be significantly different than if they were not.

Some holochroal eyes had square lenses in the lower part of the eye: *Paralejurus* (Clarkson 1975) and, as shown here, *Shizhudiscus*. Such square lenses originated as a consequence of lens-packing geometry alone. Whereas their shape might suggest that they were pre-adapted for mirror-box optics, the eye needs to be uniformly curved in order for this to work, and this is not the case in trilobites. There is an interesting, though remote parallel here between the development of the larval eye of the decapod *Palaemon serratus* and the eye of *Shizhudiscus*. Land (1981) has shown that in the larval form the eye has hexagonal facets, but as the eye develops these gradually square off. This happens late in development when the animal is two-thirds its adult size, probably relating to a change of habitat and an adult preference for dimmer deeper water. The possibility that the eyes of *Shizhudiscus* and similar forms were other than of apposition type is suggestive, though not as yet compelling. If internal structures of trilobite eyes are one day to be found the whole question can then be re-assessed.

Acknowledgements. The eight month visit of Zhang Xi-guang to Edinburgh was financed by the Sino-British Fellowship Trust and the Royal Society of London, for which we are most grateful. The SEM photographs were taken in the Faculty of Science Electron Microscope Unit, Edinburgh University, and we thank Colin MacFarlane and John Findlay for assistance. Cecilia Taylor read the manuscript and suggested a number of improvements and an anonymous referee gave helpful criticism of an earlier draft of the manuscript.

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Typescript received 4 August 1989

Revised typescript received 10 December 1989

A NEW GENUS OF ABROGRAPTID GRAPTOLITE FROM THE ORDOVICIAN OF SOUTHERN SCOTLAND

by ISLES STRACHAN

ABSTRACT. The new genus and species, *Metabrograptus scoticus*, of the family Abrograptidae is described from the Upper Ordovician (Glenkiln Shales) of southern Scotland. The new genus bears the same relationship to *Abrograptus* as *Dicranograptus* bears to *Dicellograptus*. The recognition of this further type in the family perhaps adds some weight to Finney's (1980) reference of *Reteograptus* to the Abrograptidae. Although there are problems of homologizing stipe structure, it is clear that the biserial retiolitoid condition in Ordovician forms can be derived in more than one way.

THE Family Abrograptidae was erected in 1958 by Mu to accommodate his new genus *Abrograptus* and *Dinemagraptus* Kozłowski, 1951. The family was characterized by the extreme reduction of periderm in forms with a modified dichograptid type of development and, in conformity with his views on trends in the evolution of graptolites, the family was seen as a different line from the Retiolitidae, although similarities with *Reteograptus* were noted. In particular, Mu (1958, p. 265) mentioned that the 'split specimen referred to *Retiograptus geinitzianus* Hall by Elles and Wood (1908, p. 316, fig. 209c) resembles closely *Abrograptus* in general aspect'.

This specimen (BU1336b) is on a card from the Lapworth Collection with two other specimens. One of these (BU1336a) was figured by Elles and Wood (1908, pl. 34, fig. 7d) as 'part of ventral lattice' of *R. geinitzianus*, and the third specimen (BU1336c) I presumed was the counterpart of the first. When I had them photographed recently, however, it was clear that this was a second specimen with the stipes united proximally. The card is labelled in Lapworth's writing as *Clathrograptus cuneiformis*.

In his detailed description and revision of Hall's *Reteograptus geinitzianus*, Finney (1980) pointed out the differences between *Reteograptus* and the other members of the subfamily Archiretiolitinae, in particular the simple clathrial framework and sicular details in *Reteograptus* which are very similar to those of *Abrograptus*. He therefore transferred the genus to the Abrograptidae which he emended to include biserial forms.

The genera *Parabrograptus* Mu and Qiao, 1962 (with a pair of threads from the sicular apex forming a third 'branch') and *Protabrograptus* Ni, 1981 (with the sicular lying along one stipe) have been added to the family, the former genus being also recorded from Canada (Jackson 1966). Mu and Qiao (1962) also described another new genus, *Jianshanites*, which has single filaments like *Dinamagraptus* but which shows branching. Its sicular is much stouter than in other genera of Abrograptidae.

In the absence of fusellar details of the proximal end, it is difficult to decide on the developmental type present. Kozłowski (1951) regarded *Dinemagraptus* as having dichograptid development in keeping with its simple structure and Arenig age. Mu and Qiao (1962) have added a second species, *D. sinicus*, which is of Caradocian age (*N. gracilis* zone), associated with *Abrograptus*. In their description of *Parabrograptus*, from the same horizon, they mention the occurrence of 'an additional oblique filament in the crossing canal region' which possibly indicates the presence of a second crossing canal as in isograptid or leptograptid development. The third 'branch' could then be interpreted as similar to that seen in a number of specimens of *Leptograptus* (centribrachiate

forms of Elles and Wood 1903, pls 14 and 15). *Protabrograptus* could similarly be interpreted as showing the position of the sicula seen in *Dicellograptus exilis* Elles and Wood (Strachan 1986). Finney regards *Reteograptus* as having isograptid development since he recognizes two crossing canals but notes that 'it is peculiar because all proximal thecae grow upward' (Finney 1980). In the absence of fusellar structure, it would, I think, be difficult to prove that $th2_2$ was derived from $th1_2$ rather than $th2_1$, i.e. that the development was isograptid rather than diplograptid or dicellograptid. Unfortunately, not enough is known about the development in various *Dicellograptus* and *Dicranograptus* to know how they relate to the diplograptid story.

There is a further problem with Finney's (1980) placing of *Reteograptus* in the Abrograptidae. This relates to the nature of the lists of the stipes. Finney calls them ventral lists in *Abrograptus* but Bulman (1970) regarded them as dorsal, although lateral might be the best term since they are paired on each theca. At any rate, they are simple straight or slightly curved structures with the apertural loops separating off each section of the stipe. In *R. geinitzianus*, the ventral lists of Finney are curved or angular structures which are clearly not strictly ventral since the apertural loops occur in the middle of each curved list. The upper part of the curve, above the aperture, is a cross structure between the aperture and the succeeding transverse list, while the lower part below the aperture represents the lateral boundary between the thecae. This is clearly seen in his figure of the lectotype (Finney 1980, fig. 12c) where the thecal outline is preserved. It is therefore difficult to homologize the list structure in *Abrograptus* and *Reteograptus*.

The specimen figured by Elles and Wood (1908, p. 316, fig. 209c) shows the stipe characters of *Abrograptus* and cannot easily be regarded as a broken specimen of *Reteograptus* since there is no trace of the transverse or septal lists. Their illustration of this specimen unfortunately does not show the position of the sicula. In *Abrograptus* the sicula projects above the line of the stipes as in *Dicellograptus* but another specimen in the Lapworth Collection shows a proximal end with the sicula in the lower half exactly as in *Dicranograptus irregularis* Hadding where the biserial portion consists of only two or three pairs of thecae (Strachan 1986).

While checking through the collections of the British Geological Survey in Edinburgh, I was shown a partially exposed fragment identified as *R. geinitzianus* which matched the one on the Monograph plate. At my suggestion some matrix was removed by Peter Brand and a second stipe was revealed with the proximal end like a dicranograptid. We thus have four specimens showing this character and it seems reasonable to consider them as a new genus of Abrograptidae paralleling *Dicranograptus* in the Dicranograptidae.

SYSTEMATIC PALAEONTOLOGY

Specimens numbered BU are housed in the School of Earth Sciences, University of Birmingham, the GSE specimen is in the British Geological Survey, Murchison House, Edinburgh.

Genus METABROGRAPTUS gen. nov.

Diagnosis. Rhabdosome small, represented only by clathrial framework of a biserial proximal part (of ?four thecae in the type species) and two uniserial stipes diverging at 80 to 110°; sicula sclerotized normally.

Type species. *Metabrograptus scoticus* gen. et sp. nov.

Derivation of name. *Meta* (Greek – with) and *Abrograptus* as other new genera in the family bear Greek prefixes. The specific epithet indicates the country of origin.

Stratigraphical age and distribution. Upper Ordovician, Glenkiln Shales, probably *Nemagraptus gracilis* Zone, latest Llandeilian – earliest Caradocian, from the south of Scotland.

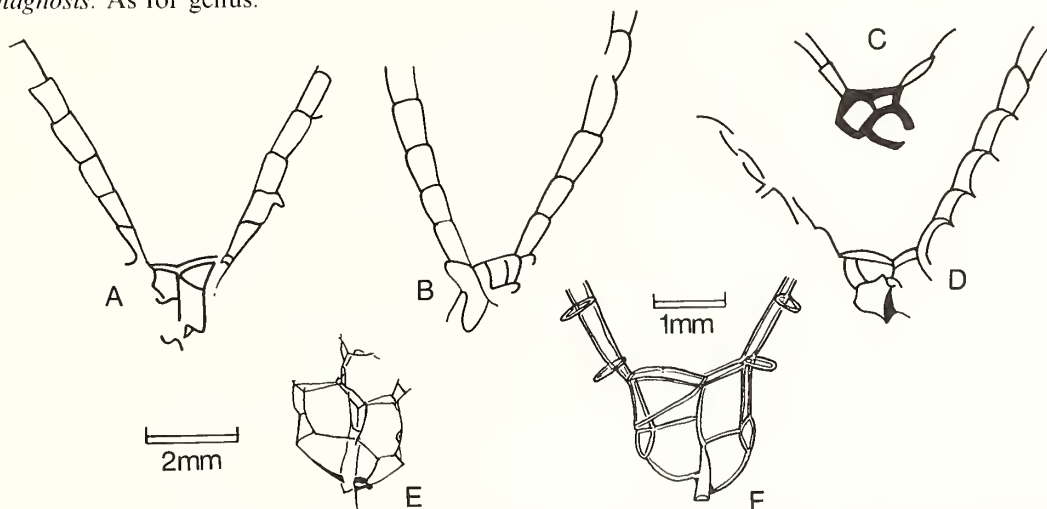
Remarks. This genus bears the same relation to *Abrograptus* as *Dicranograptus* does to *Dicellograptus*, that is, *Metabrograptus* has a short biserial portion whereas *Abrograptus* does not.

Metabrograptus scoticus gen. et sp. nov.

Text-fig. 1A–D, F

v 1908 *Retiograptus Geinitzianus* Hall; Elles and Wood (pars), p. 316, pl. 34, fig. 7d, fig. 209c.

Diagnosis. As for genus.



TEXT-FIG. 1. A–D, F, *Metabrograptus scoticus* gen. et sp. nov.: A, holotype, BU1336b; B, BU1336c; C, GSE14649; D, BU2150a; F, reconstruction of proximal end. E, *Reteograptus geinitzianus* Hall. Young growth stage, redrawn from Finney 1980, fig. 16i. All figures approximately $\times 5$, except F which is $\times 8$.

Types. Holotype, BU1336b, figured Elles and Wood, 1908, p. 316, fig. 209c. Glenkiln Shales, Birnock. Paratypes, BU1336c, same locality and horizon as holotype; BU2150a, b, locality unknown, Glenkiln Shales; GSE14649, Glenkiln Shales, Portlogan.

Description. The rhabdosome is quite small, the length of the biserial portion being 1.0 to 1.5 mm, and the stipes up to 8 mm long. The sicula appears to be normally sclerotized but details of the proximal end are poor in all specimens although they can be matched to some extent with Finney's (1980) figures of young stages of *Reteograptus* which supports its interpretation as biserial. The sicula is about 0.4 mm long. There is no distinct trace of a separate nema. The stout thread from the apex of the sicula forms part of the clathrial framework and ends at the level of the axil. A single strand from about the aperture of the sicula apparently represents the ventral line of the first theca and passes into an apertural loop. A second shorter thread connects the loop to the apex of the sicula. Above the loop, there are a pair of threads marking the lateral walls of th2¹. On the opposite side of the sicula, a thread arising a short distance above the sicular aperture represents the ventral wall of the second theca and its apertural loop is connected on the obverse side by a short thread to the 'nema' and on the reverse side by a longer oblique thread to the centre of the axil. Above the loop there are again a pair of threads marking the walls of th2².

The uniserial stipes consist of a pair of longitudinal threads divided into curved segments with apertural loops (appearing mainly as cross-bars) between the segments. The largest specimen has nine thecae on one of the stipes. The thecal spacing is 9–10 per cm. The stipes diverge at 80–110° from a broad axil which is clearly defined by paired threads in all specimens, thus differing from *Abrograptus* and *Parabrograptus* where there is only a single thread. The breadth of the axil varies from 1.4–1.6 mm, the narrower axil of BU1336c (1.1 mm) being due to oblique compression.

Remarks. Although the biserial part is badly preserved in the specimens available, comparison with Finney's (1980) growth stages of *Reteograptus* shows some strong similarities. A basic pattern of

four unequal meshes seems likely, ending in a pair of threads forming the axil which in one specimen at least can be divided into three subsections. The position of the thecal apertures is obscure but it is likely that the second pair of apertures is at the base of the uniserial stipes. An attempted reconstruction is given but much of it is speculative.

The curvature of the thecal lists shown in BU2150 is only hinted at in the Chinese figures of abrograptids which mainly show what are scalariform views of the stipes with the apertural lists appearing as cross bars. Similar views are seen in the Birnock specimens. The Portslogan example appears to be very heavily sclerotized although fragmentary but shows the same sort of contrast with the other specimens as is shown by Finney's old and young growth stages of *Reteograptus* (Finney 1980, cf. figs 13f and 16j).

The four specimens appear to be conspecific although they are from different localities. They are all clearly abrograptid in their uniserial stipe characters and distinct from previously described forms in the stout proximal end. Thus a new generic name is justified since the difference is paralleled in the Dicranograptidae. Whether the Abrograptidae should include fully biserial forms as Finney has advocated remains I think open to question. While the proximal clathrial structure which he has demonstrated in *Reteograptus* agrees well with that in *Abrograptus*, there is the problem that functionally when the periderm is reduced to a simple series of lists there is little scope for variation if the lists have a supporting function.

Associated fauna. The Birnock specimens are associated with a young specimen of *Cryptograptus tricornis* (Carruthers) and a slender stipe probably of *Nemagraptus*. The other Lapworth specimen, which is labelled *Coenograptus* (*Nema.*) *pertenuis*, has slender stipes presumably of this form as well as *Orthograptus* cf. *apiculatus* Elles and Wood, *Dicellograptus exilis* Elles and Wood, *Hallograptus* cf. *mucronatus* (Hall) and *Corynoides calicularis* Nicholson, indicating a horizon in the Glenkiln Shales.

Acknowledgements. I thank Jim Allan (St Andrews University) for photographing the specimens to provide a basis for the drawings and Peter Brand for looking out possible material from the Survey collections in Edinburgh.

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Typescript received 1 August 1989

Revised typescript received 23 October 1989

ON THE GRAPTOLITES DESCRIBED BY BAILY (1871) FROM THE SILURIAN OF NORTHERN IRELAND AND THE GENUS *STREPTOGRAPTUS* YIN

by DAVID K. LOYDELL

ABSTRACT. The graptolite faunas described by Baily in 1871 from County Down, N. Ireland are re-examined and assigned to the middle part of the *Monograptus turriculatus* Biozone of the Telychian (Upper Llandovery). One of Baily's new species, *Graptolithus plumosus*, is redescribed and a neotype selected. It is suggested that *G. plumosus* is the valid type species of the genus *Streptograptus* Yin, 1937, but was misidentified by Yin as *M. nodifer* Törnquist, 1881. An emended generic diagnosis for *Streptograptus* is given.

IN 1871 William Hellier Baily described the fossils collected during the mapping by the Geological Survey of Ireland of Sheets 49, 50 and part of 61 (including the country around Downpatrick, and the shores of Dundrum Bay and Strangford Lough, County of Down). These were exclusively graptolites and were collected from three localities only (Baily 1871): (a) Loc. 1. Railway cutting, 0.75 mile SE of Annacloy Bridge, 3 miles NW of Downpatrick; (b) Loc. 2. Ballytrustan, 4 miles E of Downpatrick; (c) Loc. 3. Tieveshilly, a little N of Carrstown Burn, 2 miles SE of Portaferry.

Baily assigned the graptolites to three species, *Graptolithus priodon*, *G. plumosus* and *G. gradatus*, the latter two of which he considered to be new species. Baily's work subsequently received scant attention in the literature, especially after Lapworth (1876) placed *G. plumosus* into synonymy with *Monograptus exiguus* Nicholson, and did not include it or *G. gradatus* in his '*Graptolites of County Down*, (Lapworth 1877).

The author has recently re-examined some of the specimens described by Baily after their location in the Ulster Museum (abbreviated BELUM) by Mr John Wilson. Apart from one slab, from Loc. 1, all the material comes from the Tieveshilly locality (Loc. 3). This re-examination has shown that *G. plumosus* is not a synonym of *M. exiguus*, and the resurrection of *G. plumosus* will solve a number of complex taxonomic problems which have been hampering the progress of Upper Llandovery graptolite research for some time. In addition, a fairly precise age for the graptolite assemblage (which includes more species than Baily originally identified) can be determined.

DESCRIPTION OF THE GRAPTOLITE FAUNA

All the graptolites are preserved in very low relief in pyrite in dark grey mudstone. There is no evidence of any tectonic distortion.

The single slab from Locality 1 bears three specimens of *Stimulograptus halli* (Barrande, 1850) (Pl. 1, fig. 7) (misidentified by Baily as *G. priodon*), two specimens of *Streptograptus plumosus* (see Systematic Palaeontology below), a proximal end of a robust pristiograptid (probably *Pristiograptus bjerringus* (Bjerreskov, 1975)), and one specimen of *Monograptus* cf. *barrandei* sensu Bjerreskov, 1975, (Pl. 1, fig. 2).

The Tieveshilly fauna comprises six species: *M. turriculatus* (Barrande, 1850) sensu lato; *M. planus* (Barrande, 1850) (Pl. 1, fig. 1) (= Baily's *G. gradatus*); an indeterminate small diplograptid;

S. plumosus; and *Stimulograptus halli* and *M. tuvaensis* Obut in Kul'kov and Obut, 1973 (Pl. 1, figs 5 and 6) (both of which had been identified by Baily as *G. priodon*).

SYSTEMATIC PALAEOLOGY

Streptograptus plumosus (Baily, 1871)

Plate 1, figs 3 and 4; Text-fig. 1

- v* 1871 *Graptolithus plumosus*; Baily, pp. 22–23, fig. 1a–c.
- vp 1913 *Monograptus nodifer* Törnquist; Elles and Wood, pp. 454–6, pl. 46, fig. 2a–d; text-fig. 313b (non a, c, d).
- 1937 *Streptograptus nodifer* (Törnquist); Yin, p. 297.
- 1943 *Monograptus* (*Streptograptus*) *exiguus primulus* Bouček and Přibyl, p. 7, pl. 1, fig. 4; text-fig. 3e–f.
- 1975 *Monograptus exiguus primulus* Bouček and Přibyl; Bjerreskov, p. 62, pl. 9, fig. D; text-fig. 18H.
- 1986 *Streptograptus nodifer* (Törnquist, 1881); Chen, pp. 134–6, pl. 1, figs 1–12; pl. 2, figs 1–12; pl. 3, figs 1–12.

Type specimen. The specimen illustrated by Baily (1871, fig. 1a–c) is no longer present within his collection. A neotype has therefore been selected: BELUM: K12275a, a proximal end with thecae up to th7 (figured herein as Pl. 1, fig. 4 and Text-fig. 1). This is from the *Monograptus turriculatus* Biozone of Tieveshilly, County Down, Northern Ireland.

Material. Approximately 100 specimens on slabs BELUM: K12274, 12275, 12277 and 12280. Many are fragmentary, but a few are more complete and include proximal ends.

Diagnosis. Rhabdosome hook-shaped; straight or very gently dorsally curved proximally, strongly ventrally curved mesially, becoming more gently ventrally curved or even straight distally. Prothecae with folds at their bases, otherwise parallel-sided. Metathecae retroverted, terminating in an upturned lip causing the central part of the thecal aperture to face proximally. Laterally, the aperture is slit-like. Dorso-ventral width increases from c. 0.4 mm at th1 to c. 0.7 mm at th30.

Description. The rhabdosome is hook-shaped, although the degree of curvature is somewhat variable. From th1 to 2 or 3 it is straight or very gently dorsally curved; to th6–9 it is strongly ventrally curved; thereafter ventral curvature is more gentle and distally the rhabdosome may appear straight. The sicula has a length of 0.95–1.2 mm and its apex reaches to from just above the top of th1 to half way up th2. Its apertural width is 0.21–0.22 mm. The thecae are uniform throughout the rhabdosome and take up approximately half of its dorso-ventral width. The bases of the thecae are expanded laterally into prothecal folds (poorly seen on this low relief material), after which the prothecae are parallel-sided. The metathecae are retroverted, but terminate in an upturned lip which causes the central part of the thecal aperture to face proximally. Laterally the aperture is very narrow and slit-like. Thecal overlap is negligible. Details of dorso-ventral and thecal spacing are given in Table 1.

EXPLANATION OF PLATE 1

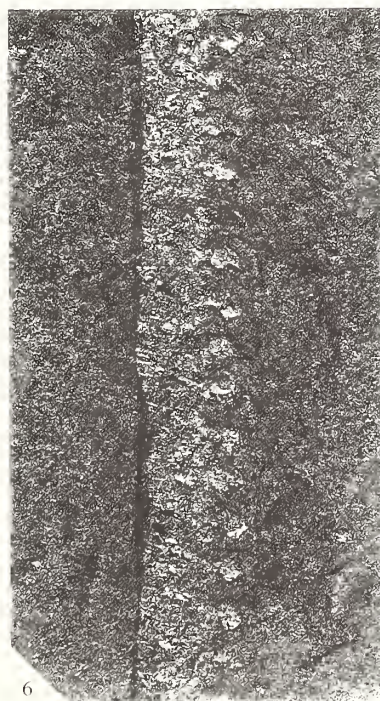
Fig. 1. *Monograptus planus* (Barrande, 1850), BELUM: K12274.

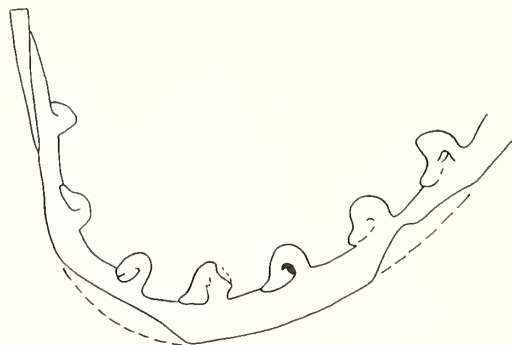
Fig. 2. *Monograptus* cf. *barrandei* sensu Bjerreskov, 1975, BELUM: K12277.

Figs 3 and 4. *Streptograptus plumosus* (Baily, 1871). 3, BELUM: K12274b. 4, BELUM: K12274d, neotype. Figs 5 and 6. *Monograptus tuvaensis* Obut in Kul'kov and Obut, 1973, BELUM: K12280. 5, proximal end. 6, distal end of same specimen.

Fig. 7. *Stimulograptus halli* (Barrande, 1850), BELUM: K12276.

All figures $\times 5$. All specimens, except *Stimulograptus halli* (Fig. 7), are from the middle part of the *Monograptus turriculatus* Biozone, Tieveshilly, County Down, Northern Ireland (Baily's 1871 Loc. 3); the specimen of *S. halli* is from the same horizon from the railway cutting, SE of Annacloy Bridge, County Down, Northern Ireland (Baily's 1871 Loc. 1).





TEXT-FIG. 1. Neotype of *Streptograptus plumosus* (Baily, 1871), BELUM: K12274d, middle *Monograptus turriculatus* Biozone, Tieveshilly, County Down, Northern Ireland, $\times 20$.

TABLE 1. Measurements of dorso-ventral width and thecal spacing (2TRD, Howe 1983) for *Streptograptus plumosus* (Baily, 1871), based on the ten specimens with proximal ends preserved in Baily's collection.

	Theca	Width (mm)	2TRD (mm)
	1	0.39–0.52	
	2	0.36–0.44	1.22–1.74
	3	0.38–0.48	1.30–1.52
	5	0.44–0.58	1.34–1.46
	10	0.51–0.56	1.30
	20	0.63–0.66	1.36–1.59
	30	0.70	1.60

Horizon. Bjerreskov (1975) records an almost identical fauna from the middle part of the *Monograptus turriculatus* Biozone (Lower Telychian, Llandovery) on Bornholm. The author has also found the same assemblage of species (except for *M. tuvaensis*) at this level in central Wales. It would seem very likely, therefore, that Baily's material is of middle *turriculatus* Biozone age.

THE GENUS *STREPTOGRAPTUS* YIN

The history of this genus is highly complex, involving, in particular, the misidentification of the type species by the author of the genus and the misinterpretation of thecal morphology in imperfectly preserved material.

Lapworth's (1876) incorrect synonymy of *Streptograptus plumosus* with his *Monograptus exiguus* is mentioned above. The species differ in terms of thecal morphology, rate of increase of rhabdosome width and stratigraphical horizon (*S. plumosus* does not range into the uppermost *turriculatus* Biozone and *M. crispus* Biozone, whereas in all correct references to *M. exiguus* the associated fauna is indicative of these horizons).

Far more serious, however, particularly when viewed in the light of later events, was the misidentification of *Monograptus nodifer* Törnquist, 1881 by Elles and Wood (1901–18) in their enormously influential *A Monograph of British Graptolites*. This work became the standard guide for graptolite identification over much of the world for the next fifty years and is still widely used. In their text-figures Elles and Wood illustrated more than one species as *M. nodifer*, but all 4 figures on their plate 46 are undoubtedly *S. plumosus* from the *turriculatus* Biozone of Aberystwyth, Wales. *M. nodifer* s.s. does not occur in this zone, but is characteristic in particular of the uppermost Telychian *Monoclimacis crenulata* Zone. Although rhabdosome form is occasionally similar to that seen in *S. plumosus*, thecal morphology in *M. nodifer* s.s. has been shown by Rickards *et al.* (1977, text-fig. 32) to be quite different.

Yin (1937, p. 297) erected the genus *Streptograptus*, for which he gave the following diagnosis: 'Polypary with dorsal, ventral or more frequently dorso-ventral curvature, thecae essentially uniform, being tubes with the whole apertural region coiled into a definite lobe and more or less twisted; overlap usually insignificant: thecal aperture visible from the obverse view.' He designated *Monograptus nodifer* Törnquist the type species of the genus. However, his specimens from Shihtien had been collected from a horizon also yielding *Monograptus turriculatus* and were thus clearly not *M. nodifer* s.s. Chen (pers. comm.) has stated that in China all references to *M. nodifer* are sensu Elles and Wood and not sensu Törnquist, and indeed this is borne out by examination of the Chinese graptolite literature. Mu *et al.* (1962), N.I.G.P. (1974), Wang *et al.* (1977), Wang (1978), Chen (1984) and Chen (1986) have all based their identifications upon Elles and Wood's (1901–18) description.

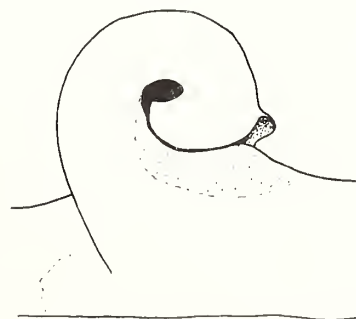
The situation was further complicated by Bouček and Přibyl (1943). They considered *Streptograptus* to be a subgenus of *Monograptus* and emended Yin's diagnosis (Bouček and Přibyl 1943, p. 3): 'Polyparium schwächer, nach innen gebogen oder s-artig gekrümmt, seltener gerade. Zellen wenigstens teilweise auf der ventralen Seite der Stöcke. Die Zellenspitzen nach innen eingerollt.' Unfortunately, the imperfectly preserved material on which they based their diagnosis resulted in a misinterpretation of the thecal apertural structure. In addition, they created a subspecies of *Monograptus exiguus* which they named *Streptograptus exiguus primulus*. This is a junior synonym of *M. plumosus* and is thus, therefore, identical to Elles and Wood's *M. nodifer*. It is accordingly surprising, as Strachan (1971, p. 54) points out, that Bouček and Přibyl placed Elles and Wood's *M. nodifer* into synonymy with *M. nodifer* sensu Törnquist (i.e. sensu stricto).

Streptograptus has subsequently been widely used outside Britain and North America, either as a genus or subgenus, for a wide variety of species having or appearing to have lobed, coiled or retroverted metathecae. These undoubtedly belong to a number of different phyletic groupings.

In Britain a very conservative attitude has quite rightly been followed with regard to the erection and use of monograptid genera and subgenera. Bulman and Rickards (1970, p. V150) state: 'The main objection to most such genera is that their erection was not accompanied by any addition to our imperfect knowledge of their morphology and phylogeny; their context is ill-defined and their application correspondingly uncertain.' This has been very much the case with *Streptograptus*. However, the time would now seem to be ripe for a re-evaluation of the situation, particularly in the light of the redescription of Baily's collection above and the description by Chen (1986) of chemically isolated specimens of *S. plumosus* (refigured herein as Text-fig. 2) originally identified by him as *Streptograptus nodifer* but now (Chen pers. comm.) recognized as *S. plumosus*.

As Yin clearly based his generic diagnosis for *Streptograptus* on *Monograptus plumosus* and not on *Monograptus nodifer* s.s., *G. plumosus* should be made the type species of the genus *Streptograptus* Yin, 1937, and the generic diagnosis should, on the basis of both Baily's (1871) and Chen's (1986) material, be emended. I propose to submit an application to the International Commission on Zoological Nomenclature to designate the nominal type species *Graptolithus plumosus* Baily, 1871 as the type species of *Streptograptus* Yin, 1937 since the original type was based on misidentified material.

TEXT-FIG. 2. Metathecal morphology of *Streptograptus plumosus* (Baily, 1871) (modified from Chen 1986, text-fig. 4) in a chemically isolated specimen, $\times 75$.



Emended generic diagnosis. Rhabdosome ventrally, dorsally or dorsoventrally curved, rarely straight. Metathecae retroverted, terminating in an upturned lip causing the central part of the thecal aperture to face proximally. Laterally the aperture is slit-like. The bases of the prothecae are usually expanded into prothecal folds. Thecal overlap insignificant. Sacula small.

This emended diagnosis would result in the genus including the following species: *Graptolithus plumosus* Bailly, 1871; *Monograptus pseudoruncinatus* Bjerreskov, 1975; *Streptograptus filiformis* Chen, 1984; *M. petilus* Hutt, 1975; *M. ansulosus* Törnquist, 1892; *M. runcinatus* sensu Perner, 1897; *Monoclimacis labialis* Chen, 1984 (= *Monograptus exiguus* A of Bjerreskov, 1975); *S. linearis* Chen, 1984; *Pernerograptus sidiachenkoi* Obut and Sobolevskaya, 1965; and a number of as yet unnamed species which have been compared to *Monograptus barrandei* sensu Elles and Wood (e.g. Hutt *et al.* 1970; Bjerreskov 1975).

M. (S.) pseudobecki Bouček and Přibyl, 1943 and *M. exiguus* Lapworth, 1876 (see Loydell 1989) probably also belong in this genus, but examination of well-preserved material will be necessary before this can be confirmed. It is worth noting here that the specimens described by Hutt *et al.* (1970) and by Bulman and Rickards (1970) as *M. exiguus* are not this species but are an as yet unnamed species with apertures laterally expanded and different to those of *Streptograptus* as defined herein. The objections of Bulman and Rickards to the genus, based on this material, are thus unfounded.

Acknowledgements. The author is very grateful to Mr John Wilson of the Ulster Museum, Belfast for arranging the loan of the specimens and for much useful information. Dr A. G. Sleeman of the Geological Survey of Ireland initially suggested to me that Bailly's graptolites might be housed there. Useful discussions were had with Prof. Chen Xu, whilst I was in Nanjing in November, 1988 regarding the *Streptograptus* problem. He also made his collections available for study. Petr Štorch kindly sent me material of *M. (S.) exiguus primulus*. Dr P. D. Taylor and an anonymous referee made useful criticisms of the original manuscript. Dr J. D. D. Smith gave advice on ICZN matters. Research for this paper was carried out while in the tenure of a University of Wales Postgraduate Studentship.

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Typescript received 15 October 1989

Revised typescript received 19 February 1990

EDIACARAN FOSSILS FROM THE SEKWI BROOK AREA, MACKENZIE MOUNTAINS, NORTHWESTERN CANADA

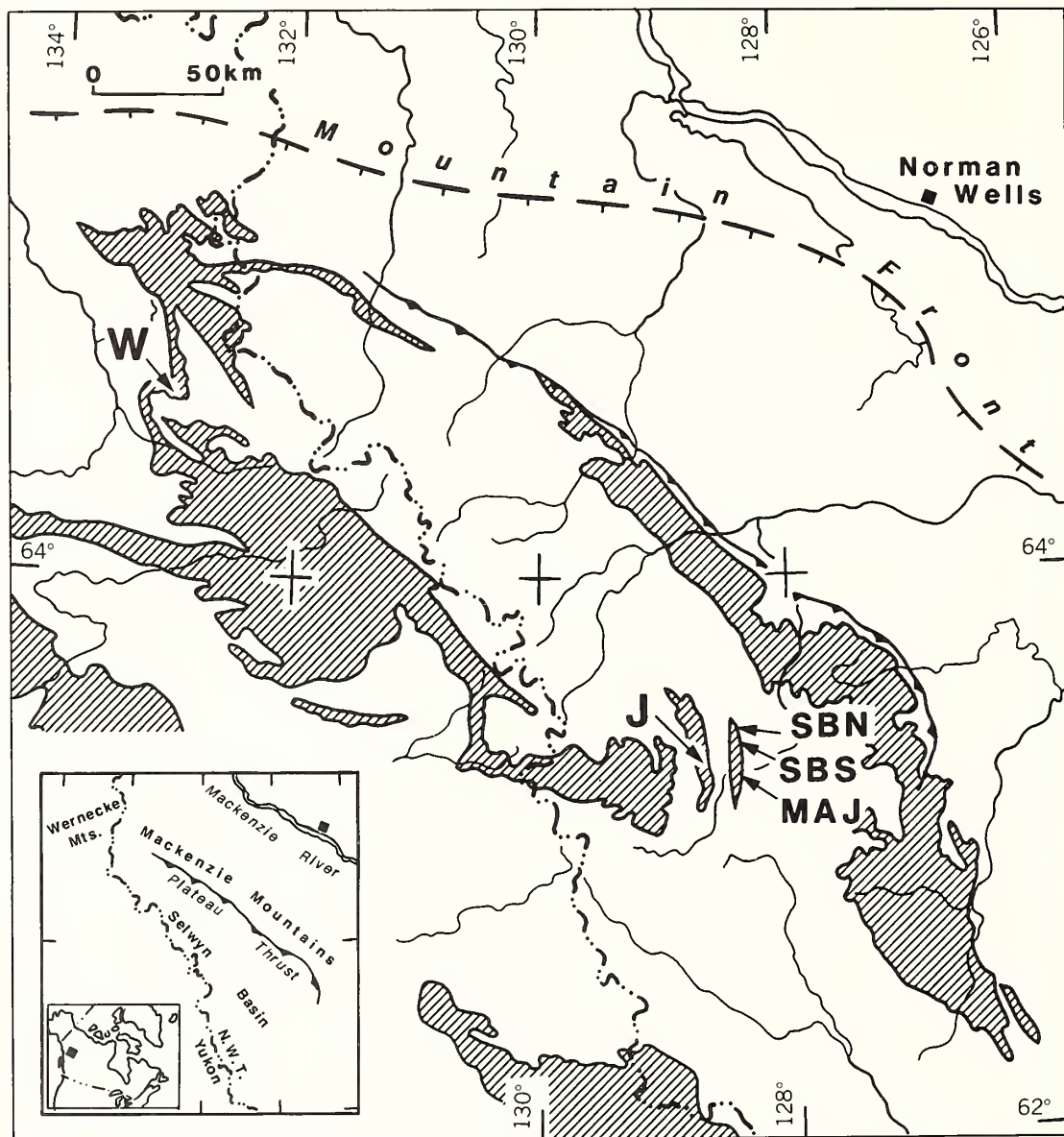
by GUY M. NARBONNE *and* JAMES D. AITKEN

ABSTRACT. Ediacaran body fossils and trace fossils occur sporadically throughout more than one kilometre of strata in the upper part of the Windermere Supergroup in the western Northwest Territories of Canada. The oldest fossiliferous unit, the Sheepbed Formation, contains body fossils (*Beltanella gilesi*, *Charniodiscus*? sp., *Cyclomedusa plana*, *Cyclomedusa* sp., *Eoporpita* sp., *Kullingia* sp. and *Medusinites asteroides*) and very rare trace fossils (*Planolites montanus*). The Blueflower Formation contains rare body fossils (*Charniodiscus*? sp., *Ediacaria* sp., *Inkrylovia* sp., *Pteridinium* sp. and *Sekwia excentrica*) and abundant trace fossils (*Aulichnites* ichnosp., *Helminthoida* ichnosp., *Helminthoidichnites tenuis*, *Helminthopsis abehi*, *Helminthopsis irregularis*, *Helminthopsis*? ichnosp., *Lockeia* ichnosp., *Neonereites* ichnosp., *Palaeophycus tubularis*, *Planolites montanus*, *Torrowangea rosei* and a knotted burrow). Overlying dolostones and thick-bedded sandstones of the Risky Formation contain only simple trace fossils (*Palaeophycus tubularis*, *Planolites montanus*). The Sekwi Brook biota lived in a deep-water, basin slope setting below storm wave-base. Most of the body fossils probably represent benthic polypoid and frond-like organisms. The body fossil assemblage is broadly similar to that described from correlative shallow shelf deposits in the Wernecke Mountains, Flinders Ranges and Russian Platform. The trace fossil assemblage is dominated by simple and irregularly meandering burrows, but contains some patterned meanders typical of the *Nereites* ichnofacies. The occurrence of this relatively diverse, mainly deep-water assemblage of benthic body fossils and infaunal burrows indicates that the initial radiation of metazoans extended to the deep sea, and that some aspects of Phanerozoic-style marine ecosystems were initiated during the earliest stages of metazoan evolution.

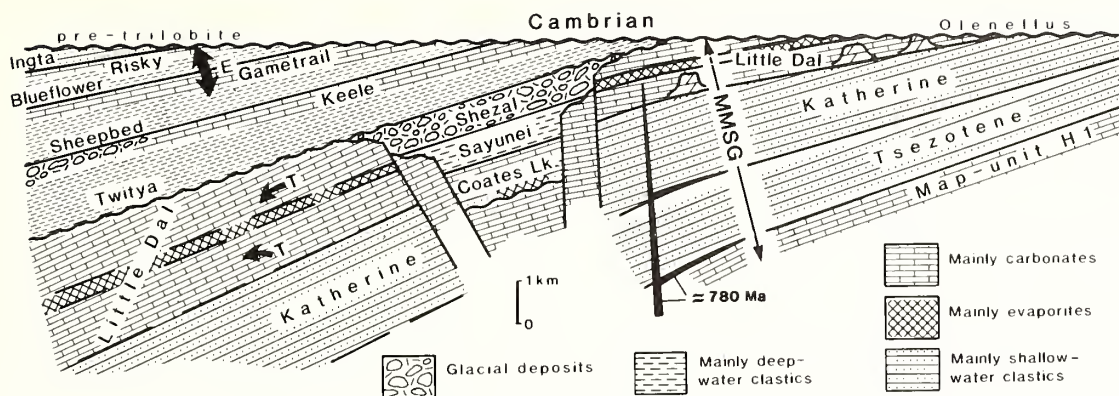
THE Ediacaran fauna represents the oldest diverse assemblage of megascopic animals and trace fossils in the world, and consequently the rootstock from which all subsequent metazoans evolved. Ediacaran animal remains are predominantly discoid and pennate fossils (commonly interpreted as primitive cnidarians) with fewer arthropods, echinoderms and problematic taxa. Trace fossils are chiefly simple subhorizontal burrows with rarer meandering forms. Recent summaries of this fauna can be found in Glaessner (1984) and Sokolov and Ivanovskiy (1985).

The Ediacaran assemblage is of latest Precambrian age, and consistently occurs between the highest Proterozoic tillites and the lowest Cambrian-type shelly fossils and trace fossils (Jenkins 1981; Cloud and Glaessner 1982; Sokolov and Fedonkin 1984). It was first reported from Namibia and South Australia, but subsequently has been documented from more than twenty-five localities around the world (Glaessner 1984, fig. 1/8; Hofmann 1987, fig. 13). The first description of Ediacaran fossils from Laurentia (= ancestral North America) was by Hofmann (1981), who collected body fossils and trace fossils from the Sekwi Brook area of the Mackenzie Mountains (Text-fig. 1) during a brief visit of the I.U.G.S. Precambrian–Cambrian Boundary Working Group (Fritz 1980). Hofmann reported the body fossils *Inkrylovia* sp. and *Sekwia excentrica*, the trace fossils *Torrowangea* sp. and *Gordia* sp. and several problematica and dubiofossils. Aitken (1989a) subsequently figured a specimen of the megafossil *Pteridinium* sp. from the same locality, Baudet *et al.* (1989) studied the acritarchs from this section, and Aitken and Narbonne (1989) described cryptalgal structures from a nearby section. Ediacaran body fossils and ichnofossils have also been described from age-equivalent shallow shelf deposits in the Wernecke Mountains (Text-fig. 1), 250 km west north-west of Sekwi Brook (Hofmann *et al.* 1983; Narbonne and Hofmann 1987).

During June 1988, the present authors collected Ediacaran fossils from Hofmann's (1981) locality and two others in the Sekwi Brook area of the Mackenzie Mountains (Text-fig. 1) as part of a regional study of the upper Precambrian strata. These collections considerably extend the known diversity and stratigraphic range of Ediacaran fossils in the Mackenzie Mountains. Previous reports of Ediacaran fossils have been mainly from shallow shelf settings (e.g. Flinders Ranges, Russian Platform, Wernecke Mountains) with fewer reports from deep slope/fan environments (e.g. Newfoundland, Charnwood Forest). The occurrence of a relatively diverse assemblage of body



TEXT-FIG. 1. Location of study sections in the Mackenzie Mountains. Outcrop of the Windermere Supergroup is shaded. SBN = Sekwi Brook North; SBS = Sekwi Brook South; MAJ = Majesty Property. Other fossiliferous Ediacaran sections described previously are in the June Lake Anticline (J) and in the Wernecke Mountains (W).



TEXT-FIG. 2. Regional stratigraphic setting of the Ediacaran biota from Sekwi Brook. E = Ediacaran fossils; T = *Chuarina-Tawuia* assemblage; MMSG = Mackenzie Mountains Supergroup.

fossils and trace fossils in basin slope deposits at Sekwi Brook permits more detailed evaluations of the palaeoenvironmental affinities of Ediacaran organisms. In this paper, description of the fossils and discussion of their significance are by Narbonne; information on the stratigraphy and depositional environments of the strata is by Aitken.

STRATIGRAPHIC AND PALAEOENVIRONMENTAL SETTING

The terminal Proterozoic formations of the Mackenzie and Wernecke Mountains (Text-figs 1 and 2) are assigned to the upper part of the Windermere Supergroup. The base of the Windermere is marked by the onset of rifting at 770–780 Ma (Armstrong *et al.* 1982; Eisbacher 1981, 1985; Jefferson and Ruelle 1986). The top is the base of Cambrian strata.

The terminal Windermere Formations make up four, kilometre-scale, shallowing-upward, carbonate-capped Grand Cycles (*sensu* Aitken 1966, 1978), as follows (Aitken 1989a):

4. Ingta Formation (230 m)
3. Blueflower (550 m) and Risky (150 m) Formations
2. Sheepbed (900 m) and Gametrail (300 m) Formations
1. Twitya (900 m) and Keele (500 m) Formations

These cyclical deposits post-date, and pass without noticeable effect, across the sites of the rift-depressions in which the older Windermere deposits, the Coates Lake and Rapitan groups, were deposited (Text-fig. 2). Evidence for a Rapitan glaciation is well known (Young 1976; Yeo 1981; Eisbacher 1981, 1985). The deposits of a second Late Proterozoic glaciation, which directly underlie the Sheepbed Formation, have thus far been described only in oral presentations with published abstracts (e.g. Aitken 1987, 1989b).

The middle two of the upper Windermere Grand Cycles (Sheepbed-Gametrail, Blueflower-Risky) contain abundant Ediacaran megafossils (this study). The uppermost Windermere Grand Cycle, the Ingta Formation, yields abundant, well-preserved trace fossils, but lacks both diagnostically Cambrian traces and body impressions of Ediacaran type. We interpret it as latest Precambrian. The Ingta, and in other places all of the other terminal Proterozoic formations, are unconformably overlain by correlatives of the Backbone Ranges and Vampire Formations bearing Early Cambrian trace fossils and small shelly fossils (Fritz *et al.* 1983; Narbonne *et al.* 1985; Nowlan *et al.* 1985). The position, in basinward areas such as Sekwi Brook, of the major unconformity beneath the typical Backbone Ranges Formation is in dispute (reviewed by Aitken 1989a).

Sheepbed Formation

The Sheepbed Formation of the Sekwi Brook area is much coarser, on average, than in the 'typical' belt of exposures above the Plateau Thrust. The lower part, below the lowest fossils found, contains rare packets of thick and very thick beds of quartzose sandstone that are normally graded and in part coarse-grained (Bouma

Ta). Rare packets of ribbon-bedded lime mudstone are also present. Because of their association with and involvement in mass-transport deposits, and normal grading seen in minor beds with a content of coarser allochems, they are interpreted as turbidites. The upper (fossiliferous) part is dominated by laminated to finely laminated, dolomitic siltstone and very fine-grained sandstone, with partings and packets of dark grey to brown, silty shale and mudstone. Sole marks are present, but rare. The thin sandstones are Bouma Tb, Tbc, and Tc units. The content of dolomitized and undolomitized, ribbon-bedded lime mudstone (turbidites), monomict, matrix-supported carbonate breccias (debris flows), and penecontemporaneous folds and slide masses is highly variable along strike. The thickness in the Sekwi Brook area is not determinable, but is almost certainly greater than the maximum of 800 m in the 'typical' outcrop belt.

Interpretation of the depositional environment begins with the observation that the 'typical' Sheepbed to the north-east contains very little sand-grade or coarser siliciclastic material. The Gametrail Formation (carbonates, there partly in a shallow-water facies) that intertongues with and overlies the upper Sheepbed, also lacks siliciclastic detritus. The 'typical' Sheepbed overlies the deeply drowned Keele platform, whereas Sekwi Brook lies outboard of the Keele platform margin, above a previously-existing bathymetric basin or trough. It is precisely at Sekwi Brook that coarse-grained, thick-bedded, turbiditic sandstones occur in the lower Sheepbed. These sandstones appear to be deep-sea fan-channel deposits (Mutti and Normark 1987; Shanmugam and Moiola 1988), transported axially along the inherited off-platform trough. The upper part of the formation is readily interpreted as a complex of slope deposits that accumulated below storm wave-base. This is consistent with the character of the overlying Gametrail carbonates at Sekwi Brook, which are of ribbon-bedded facies, interrupted only by monomict, matrix-supported, debris-flow breccias and slide masses. Thus, in the Sekwi Brook area, southwestward-prograding slope deposits (upper Sheepbed, Gametrail) appear to have buried axially prograding deep-sea fan deposits (lower Sheepbed).

Blueflower Formation

The Blueflower Formation is not preserved above the Sheepbed and Gametrail formations of the 'typical' outcrop belt (Text-fig. 2). At Sekwi Brook it is 550 m thick, and consists of dark-coloured, deep-water shale and mudstone (59%), turbiditic sandstones (15%), and limestones of turbiditic and grain-flow origin (26%). It is the lower part of a shoaling-upward cycle that terminates with the peritidal dolomites of the overlying Risky Formation. Other upward trends within the Blueflower are: decrease and virtual disappearance of carbonate beds; increase in the proportion of sandstone; and the appearance, near the top, of non-turbiditic sandstones with low-angle cross-stratification.

Sandstones in the lower three-quarters of the formation are predominantly thin-bedded, fine-grained turbidites (Bouma Tb, Tc, and Tbc), with a few thicker and generally coarser beds that are Bouma Ta and Tab units, and structureless beds interpreted as liquefied-flow deposits (Lowe 1982). Flame structures are common, flute and groove casts less so. Thin sandstone beds are persistent across the typical widths of the gully outcrops (50 m), but bundles of such beds are markedly lenticular over distances of 200–400 m.

Limestones occur in packets of two types: ribbon-bedded lime mudstone, in part displaying flame structures and normal supply-grading of a sparse content of quartz sand grains; and subordinate, markedly lenticular packets of medium and thick beds of intraclast grainstone and wackestone with a variable content of quartz sand grains. Most of the latter display normal grading, and are Bouma Tab and Tb units. The packets of ribbon-bedded limestone are distinctly lenticular over distances of less than one kilometre.

Evidence of deposition on a slope is common. It includes penecontemporaneous folds, detached fold-noses in dismembered sandstone beds, scoop-shaped slide surfaces, contorted and mixed mudstone units with deformed pods of sandstone, matrix-supported debris-flow breccias, at least two slide masses or debris-flow paraconglomerates with boulders of shallow-water carbonate rocks, rare exotic blocks and boulders, and, high in the type section, an exotic raft of stromatolitic dolomite.

The overall aspect of the lower three-quarters of the Blueflower at Sekwi Brook is that of a slightly channelled slope below storm wave-base. The content of thin-bedded turbidites, with thickening-upward and less common thinning-upward sequences, might suggest the middle to lower parts of a deep-sea fan. Indeed, a lens of thick-bedded, massive sandstone cropping out less than one kilometre north of the type section resembles a fan-channel deposit. The abundant evidence of slope deposition is, however, inconsistent with a fan interpretation overall. Because it characterizes the middle and upper parts of the formation, it probably records a depositional slope prograding above a fan-complex.

Towards the top of the Blueflower Formation, carbonate rocks reappear as blocks, boulders and rafts of limestone and dolomite of shallow-water origin. These document the progradational approach of a re-established carbonate platform, the Risky Formation, which appears at a gradational contact.

Summary

Thus it is apparent that most of the Ediacaran fossils at Sekwi Brook occur in strata deposited in a deep-water, basin slope setting considerably below storm wave-base. This is in marked contrast with the shallow-shelf assemblages in the nearby Wernecke Mountains (Narbonne and Hofmann 1987). The occurrence of assemblages of shallow- and deep-water Ediacaran fossils in localities only 250 km apart, within a single depositional and structural province, permits analysis of their bathymetric affinities, without the palaeogeographic uncertainties inherent in comparisons between distant areas.

FOSSIL OCCURRENCE AND PRESERVATION

Fossils were collected from three sections (Text-fig. 1) in the Sekwi Brook structural panel (*sensu* Aitken 1989a). The stratigraphy and distribution of fossils in the two main sections, Sekwi Brook North and Sekwi Brook South, is shown in Text-figures 3 and 4. Sekwi Brook North contains the type sections of the Gametrail, Blueflower and Risky Formations (Aitken 1989a); Sekwi Brook South was one of the sections investigated during the 1979 visit of the PreCambrian–Cambrian Boundary Working Group (Fritz 1980), and is the section where Hofmann (1981) described the first Ediacaran fossils discovered in western North America. In addition to these two main sections, trace fossils were collected from the lower half of the Blueflower Formation (locality 29), and trace fossils and body fossils were collected from the upper half of the Blueflower Formation (locality 30) during reconnaissance investigation of the Majesty Pb–Zn–Ag Property (Text-figs 1 and 4).

Some of the collections were made from outcrop, but most were from very local float (frost-heaved but effectively untransported slabs). The only exception is the figured specimen of *Ediacaria* sp., which was in float that had slid a considerable distance downhill, but which was tied into the section on the basis of the unique lithology and the presence of a fragmentary specimen of the same taxon in the same lithology at locality 27. Float that could not be tied down definitely stratigraphically was not included in the study material. The type of collection at each locality is shown in Text-figure 3.

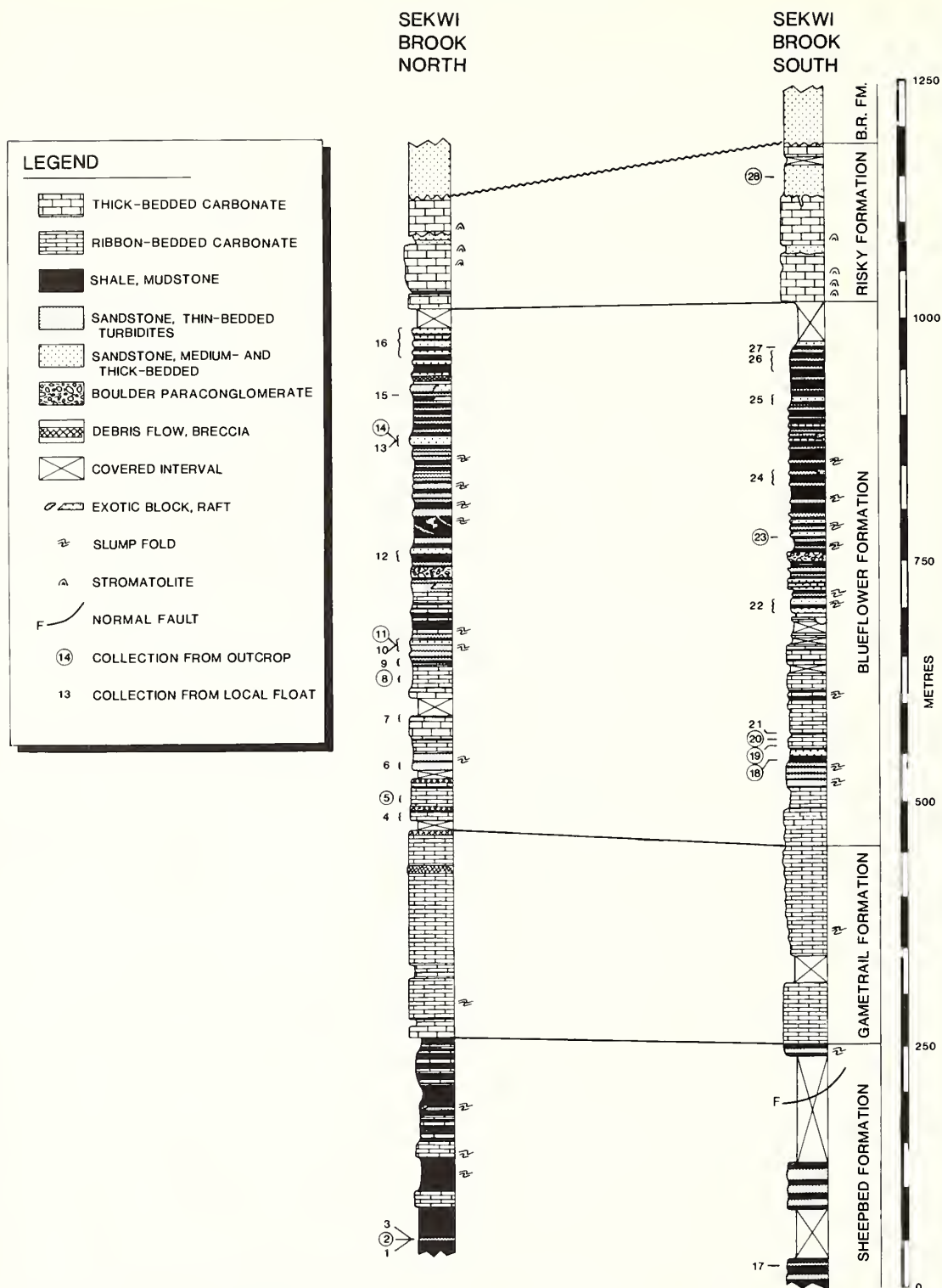
Ediacaran body fossils occur predominantly as raised features on the bottoms of beds (positive hyporelief) and very rarely as depressed features on soles (negative hyporelief). Trace fossils also exhibit the same modes of preservation, or occur as raised or depressed features on the tops of beds (positive/negative epirelief).

DISCUSSION

Body fossils

Previous reports of Ediacaran body fossils from the Sekwi Brook area by Hofmann (1981) and Aitken (1989a) were from the lower and middle parts of what is presently regarded as the Blueflower Formation. Our discoveries of specimens of *Charniodiscus* and *Ediacaria* near the top of this formation and of a relatively diverse assemblage of Ediacaran body fossils approximately 225 metres below the top of the Sheepbed Formation considerably extends the known diversity and stratigraphic range of these fossils in the Mackenzie Mountains. Ediacaran body fossils have been reported by Narbonne and Hofmann (1987) from the 'Goz Siltstone' in the Wernecke Mountains, a unit tentatively correlated with the Sheepbed Formation (Narbonne *et al.* 1985), but the present paper represents the first confirmed report of an Ediacaran biota from the Sheepbed Formation. This is significant, as this unit is geographically widespread (Eisbacher 1981) and immediately overlies the highest Proterozoic glacial deposits in northwestern Canada (Aitken 1987, 1989b).

Ediacaran body fossils occur sporadically throughout approximately one kilometre of strata (upper Sheepbed Formation to the top of the Blueflower Formation) in the Sekwi Brook area of the Mackenzie Mountains. A total of ten genera comprising eleven species are now known from these strata (Text-fig. 4). The assemblage is broadly similar to that reported by Narbonne and Hofmann (1987) from equivalent strata in the Wernecke Mountains 250 kilometres to the west (Text-figs 5 and 6). Six genera (*Beltanella*, *Charniodiscus*?, *Cyclomedusa*, *Ediacaria*, *Kullingia*?, and *Medusinites*) are common to both areas. Six genera (*Beltanelliformis*, *Nadalina*, *Rugoconites*?, *Spriggia*, *Tirasiana*, and *Vendotaenia*?) are reported only from the Wernecke Mountains, and four genera (*Eoporpita*, *Inkrylovia*, *Pteridinium*, and *Sekwia*) are thus far known only from Sekwi Brook. Of the geographically restricted taxa, only *Beltanelliformis* is common, and the absence of the other



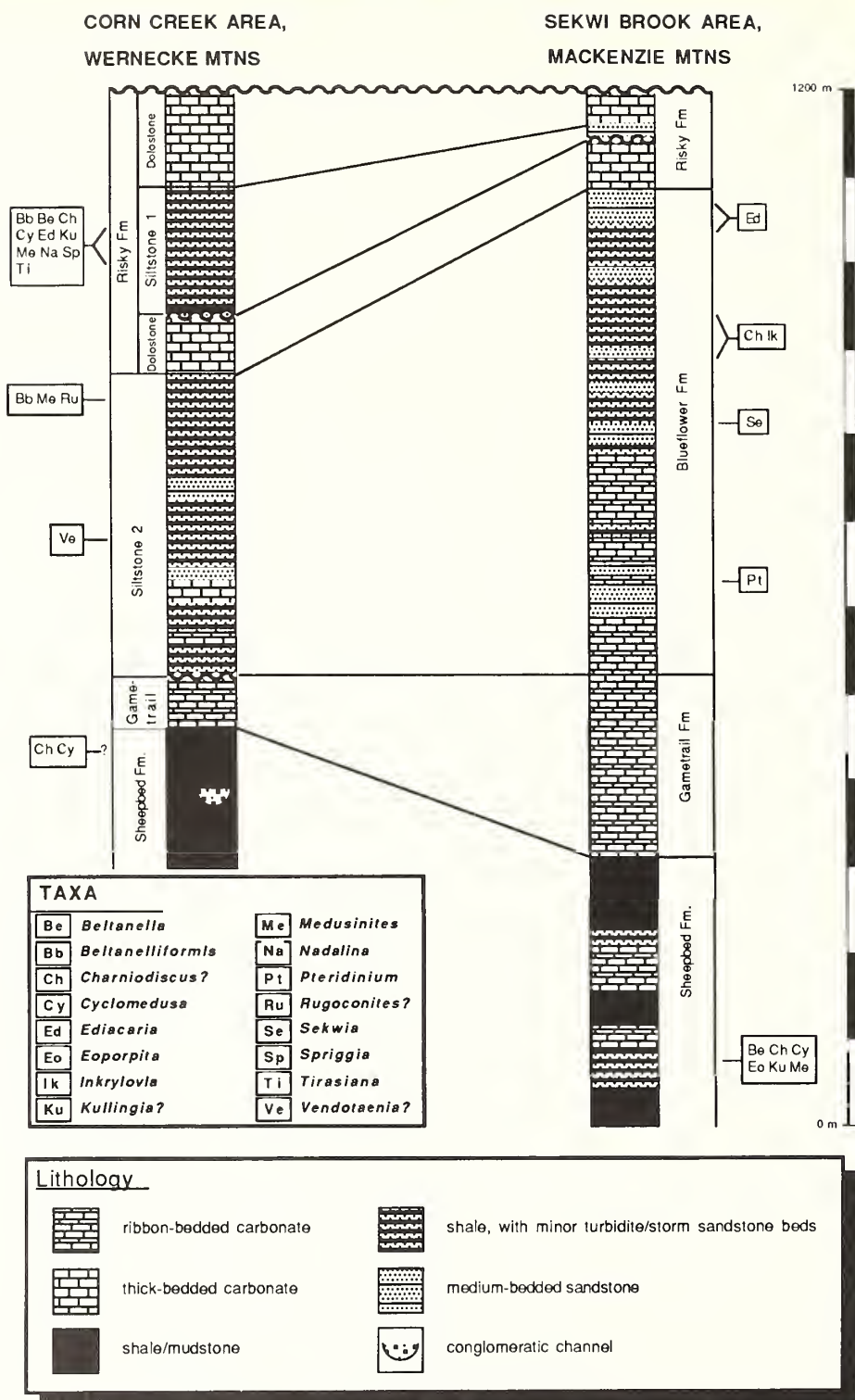
TEXT-FIG. 3. Stratigraphic sections and sample localities. B.R. FM. = Backbone Ranges Formation.

TAXA	STRATIGRAPHY			LOCALITIES																													
	Sheep-bed	Blue-flower	Risky	Sekwi Brook North															Sekwi Brook South												Majesty		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30			
BODY FOSSILS																																	
<i>Beltanella gilesi</i>																																	
<i>Charniodiscus?</i> sp.																																	
<i>Cyclomedusa plana</i>																																	
<i>Cyclomedusa</i> sp.																																	
<i>Ediacaria</i> sp.																																	
<i>Eoporpita</i> sp.																																	
<i>Inkrylovia</i> sp.																																	
<i>Kullingia?</i> sp.																																	
<i>Medusinites asteroides</i>																																	
<i>Pteridinium</i> sp.																																	
<i>Sekwia excentrica</i>																																	
Plumose problematicum																																	
ICHNOFOSSILS																																	
<i>Aulichnites</i> ichnosp.																																	
<i>Helminthoida</i> ichnosp.																																	
<i>Helminthoidichnites tenuis</i>																																	
<i>Helminthopsis abeli</i>																																	
<i>Helminthopsis irregularis</i>																																	
<i>Helminthopsis?</i> ichnosp.																																	
<i>Lockeia</i> ichnosp.																																	
<i>Neonereites?</i> ichnosp.																																	
<i>Palaeophycus tubularis</i>																																	
<i>Planolites montanus</i>																																	
<i>Torrowangea rosei</i>																																	
Knotted burrow																																	

TEXT-FIG. 4. Synopsis of Ediacaran macrobiota from the Sekwi Brook region.

taxa may simply reflect the relatively short periods of time devoted to collecting in these remote regions. Thus, it would appear that the faunas from the Wernecke and Mackenzie Mountains can be regarded as part of a single 'Windermere fauna' that characterizes the Ediacaran of northwestern Canada, and may also include the low diversity fauna described by Hofmann *et al.* (1985) from the southern Canadian Rocky Mountains.

A tentative correlation of the formations and body fossils of the Wernecke and Mackenzie Mountains is shown in Text-figure 5. With the exception of the middle siliciclastic unit of the Risky Formation, which at Sekwi Brook consists entirely of thick-bedded dolomitic sandstone and thus represents an unfavourable facies for preservation, all units that contain Ediacaran fossils in the Wernecke Mountains have fossiliferous correlatives in the Mackenzie Mountains. However, fossil assemblages in correlative units are not particularly similar, and the greatest faunal similarity is between the youngest fossiliferous unit in the Wernecke Mountains and the oldest fossiliferous unit in the Mackenzie Mountains! This suggests that most of the apparent geographical and



TEXT-FIG. 5. Correlation of Ediacaran strata and megafossils in the eastern Werneck Mountains and in the Sekwi Brook area of the Mackenzie Mountains. Lithological correlations are from Aitken (1989a, fig. 7); faunal lists are from Narbonne and Hofmann (1987) and the present study.

stratigraphic variation in the Windermere fauna reflects palaeoenvironmental and preservational factors, and an original patchy distribution, rather than palaeogeography and evolution. This view is supported by the great variation in the faunal content of equivalent strata in adjacent sections (cf. Narbonne and Hofmann 1987, text-figs 2 and 3; this study, Text-figs 3 and 4), even where the sections are within sight of each other. For this reason, we believe that any attempt to subdivide the Windermere fauna into biostratigraphic zones would be premature at the present time.

Global correlation of the Windermere body fossils is summarized in Text-figure 6. Close similarities are evident between the faunas of the Wernecke and Mackenzie Mountains, the Ediacara Member of the Rawnsley Quartzite in South Australia, and the Redkino 'Series' of the Vendian in northern Europe and Podolia. The Windermere biota is considerably less diverse than those reported from the other two regions, and apparently lacks segmented forms such as *Spriggina* and *Dickinsonia*, which are present in South Australia and on the Russian Platform. This may relate to the relatively early stages of investigation in northwestern Canada, a palaeogeographic separation between Laurentia and the latter-mentioned two areas (see McMenamin and McMenamin 1990), or some other palaeoecological or stratigraphic factor. Nevertheless, the high proportion of Windermere taxa that are also known from the type Ediacaran and the type Vendian (Text-fig. 6), emphasizes the considerable correlation potential of the Ediacaran fauna.

Baudet *et al.* (1989) concluded that the acritarchs of the Sheepbed and Blueflower Formations best correlate with the Kotlin 'Series' of the Vendian on the Russian Platform. This contradicts the above correlation, as the macrofossils of these formations are much more similar to the fossil assemblage of the Redkino 'Series' (see above) than they are to those of the overlying Kotlin 'Series', which lacks identifiable megafossils (Sokolov and Fedonkin 1984). The stratigraphic setting of these units, immediately overlying a diamictite unit and two or more Grand Cycles (400–1200 m) below the lowest Cambrian-type fossils (*Phycodes pedum* Zone), is also quite similar to that of the Redkino 'Series' and supports the correlation based on macrofossils. On the basis of published descriptions of the body fossils, ichnofossils, small shelly fossils, and the overall stratigraphic sequence, Narbonne *et al.* (1987, fig. 8) concluded that the probable equivalents of the Kotlin 'Series' in the Mackenzie Mountains are the upper part of the Risky Formation and the overlying Ingta Formation. Baudet *et al.* (1989) were unable to date these latter units, as they did not yield diagnostic acritarchs in their study. Thus, the majority of the evidence suggests that the Sheepbed, Gametrail, Blueflower and lower Risky Formations are equivalent to the Redkino 'Series' of the Vendian, and that the upper Risky and Ingta formations are equivalent to the Kotlin 'Series'.

Until recently, it was generally believed that the Ediacaran fauna was dominated by discoidal pelagic medusoids (e.g. Sprigg 1947, 1949; Glaessner and Wade 1966). Fedonkin (1985a) and Jenkins (1988) have reinterpreted many of the forms as benthic 'polyps', and this interpretation also seems to be appropriate to the Windermere biota. With the possible exception of *Kullingia*?, the fauna is entirely dominated by benthic organisms, both in terms of numbers and diversity (see Systematic Palaeontology below). The shapes of many Ediacaran organisms and their common occurrence in shallow-water facies has led some authors to suggest that they may have been partly or completely photoautotrophic (e.g. McMenamin 1986), but this is not consistent with their occurrence in muddy slope deposits considerably below storm wave-base in the Sekwi Brook area.

The Sekwi Brook fauna represents the first report of an Ediacaran assemblage in a basin slope setting. The Sekwi Brook fauna is markedly different from those reported from the deep slope/fan 'Avalon assemblage' of Newfoundland (e.g. Anderson and Conway Morris 1982), Charnwood Forest (e.g. Ford 1980), and the Carolina Slate Belt (Gibson *et al.* 1984), with only two or three of the reputedly more than twenty forms from these settings also present at Sekwi Brook. It is presently uncertain how much of this difference is palaeoenvironmental, and how much reflects palaeogeography. A closer similarity exists between the basin slope faunas from Sekwi Brook and those reported from shallow shelf deposits in the Wernecke Mountains, Flinders Ranges, Podolia, northern Europe and elsewhere (Text-fig. 6). This implies that some elements of the Ediacaran fauna extended over a considerable depth range.

TAXA		NORTHWESTERN CANADA		GLOBAL COMPARISONS										
		SHALLOW SHELF	BASIN SLOPE	SHALLOW SHELF							DEEP SLOPE/FAN			
				VENDIAN				EDIACARAN		OTHERS				
				Wernecke Mtns.	Sekwi Brook	Northern Europe	Podolia	Urals	Siberia	Flinders Ranges	Central Australia	Namibia	Central England	North Carolina
BODY FOSSILS	<i>Beltanella</i>					□			□					
	<i>Beltanelliformis</i>			□	□	□	□	○		○	□			
	<i>Charniodiscus?</i>			□				□		□		□		
	<i>Cyclomedusa</i>			□	□		□			□		○		
	<i>Ediacaria</i>			□	□			□						
	<i>Eoporpita</i>			□				□						
	<i>Inkrylovia</i>			□										
	<i>Kullingia?</i>			□	□		□		○					
	<i>Medusinites</i>			□	□		○	□						
	<i>Nadalina</i>													
	<i>Pteridinium</i>			□	□			□		□			□	
	<i>Rugoconites?</i>							□						
	<i>Sekwia</i>													
	<i>Spriggia</i>							□						
	<i>Tirasiana</i>				□	□				○				
	<i>Vendotaenia?</i>			○	○		○							
ICHOFOSSILS	<i>Aulichnites</i>			□										
	<i>Helminthoida</i>			□				○						
	<i>Helminthoidichnites</i>			□	□			□					□	
	<i>Helminthopsis</i>												□	
	<i>Lockeia</i>													
	<i>Neonereltes?</i>			□	□			○					□	
	<i>Palaeophycus</i>				○									
	<i>Planolites</i>			□	□			□	□	□			□	
	<i>Torrowangea</i>			□									○	

TEXT-FIG. 6. Regional and global correlation of the Windermere biota. Localities with less than two Windermere-type taxa are omitted. Abundance symbols for northwestern Canada: narrow bar = rare (present in < 10 % of fossiliferous units); intermediate bar = common (present in 10–50 % of fossiliferous units); broad bar = abundant (present in > 50 % of fossiliferous units). For global comparisons, same (square) or similar (circle) forms indicated.

Ichnofossils

A relatively diverse assemblage of trace fossils is present in the Ediacaran strata of the Sekwi Brook area (Text-figs 4 and 6). Previously, the oldest known trace fossils in northwestern Canada were

from the Blueflower Formation (Hofmann 1981; Aitken 1989a) and its stratigraphic equivalent in the Wernecke Mountains (Narbonne and Hofmann 1987). The occurrence of specimens of *Planolites montanus* in the upper part of the Sheepbed Formation extends the stratigraphic range of trace fossils downwards by approximately 500 metres. The Blueflower Formation contains a more diverse assemblage of trace fossils, comprising at least twelve ichnospecies referable to nine ichnogenera. All taxa known from the Ediacaran of Sekwi Brook also range the Phanerozoic. Forms restricted to the Ediacaran (e.g. *Harlaniella*, *Palaeopascichnus*, *Nenoxites*, etc.) have not yet been documented from Sekwi Brook.

Seilacher (1964, 1967) first suggested that trace fossils show a consistent ecological zonation throughout the Phanerozoic which he subdivided into several 'universal ichnofacies'. Although numerous studies have supported and refined Seilacher's model (see Ekdale *et al.* 1984 and references therein), it remains uncertain when and how ichnofacies first developed. Most of the ichnotaxa at Sekwi Brook also occur in shallower water deposits in the Ediacaran of the Wernecke Mountains, eastern and northern Europe, and Australia, and in deep slope/fan deposits in the Carolina Slate Belt (Text-fig. 6). This supports the view of Crimes and Anderson (1985) that upper Precambrian–Lower Cambrian trace fossil assemblages show a lower degree of palaeo-environmental differentiation than do those in post-Cambrian strata.

Basin slope deposits at Sekwi Brook also contain abundant simple burrows (e.g. *Planolites* and *Palaeophycus*), and non-directed meanders (especially *Torrowangea* and *Helminthoidichnites*); patterned meanders occur rarely (*Helminthoida*) to commonly (*Helminthopsis*). The presence of an assemblage dominated by meandering forms and apparently lacking vertical burrows and arthropod traces is reminiscent of the *Nereites* ichnofacies of Seilacher (1964, 1967). The *Nereites* ichnofacies typifies turbiditic slope deposits of Phanerozoic age but had not previously been reported from the Precambrian. The comparatively low diversity, the apparent absence of graphoglyptids, and the dominance of unpatterned and simple patterned forms among the meandering burrows of the Blueflower (basin slope) assemblage implies that this Precambrian assemblage represents a relatively simple version of the ichnofacies, and is consistent with Seilacher's (1974, 1977) observation that the *Nereites* ichnofacies exhibits a step-wise increase in all three of these features throughout the Phanerozoic. Previous evolutionary models for trace fossils (e.g. Crimes 1974; Seilacher 1974, 1977; Frey and Seilacher 1980) have generally concluded that deep-water slopes of Ediacaran/Vendian age were all but completely devoid of infaunal animal life, but the new evidence from the Carolina Slate Belt (Gibson 1989), the Avalon Zone of Newfoundland (pers. comm. M. M. Anderson 1989) and the Sekwi Brook area (this study) indicates that the initial radiation of metazoans also extended to the sediments of the deep-sea.

Previous workers (e.g. Crimes and Anderson 1985) suggested that complexly meandering burrowers first evolved in shallow-water settings in the early Cambrian, and later migrated into deeper-water settings. It now appears more likely that meandering burrowers originated in the Precambrian, where they occurred in both shallow marine (Glaessner 1969; Fedonkin 1985c) and deep marine (this study) settings. The explosive diversification of shallow-water burrowers in the early Cambrian, including the first appearance of abundant complexly branching, spreiten-bearing, and deep vertical burrows (cf. Alpert 1977; Crimes 1987; Narbonne *et al.* 1987), gradually eliminated meandering burrowers, especially forms producing complex meanders, from shallow-water settings. However, a low diversity assemblage of meandering burrows persisted in deeper-water slope settings, and gradually increased in diversity and burrow complexity throughout the remainder of the Phanerozoic.

SYSTEMATIC PALAEOONTOLOGY

Although genus- and species-level identification of Ediacaran organisms are relatively stable, no classification of family and higher taxonomic levels has yet been accepted. Conway Morris (1985) has argued that attempts to relate Ediacaran organisms to extant phyla and classes may obscure the relationships among these early metazoans, and even the assignment of some Ediacaran fossils to

the Metazoa has been questioned by Seilacher (1984, 1989). Rival classification schemes are presented in Pflug (1972), Glaessner (1979), Seilacher (1989), Fedonkin (1985*b*), Gureev (1987) and other papers. A full evaluation of these proposals is beyond the scope of this study, and the Sekwi Brook fossils are simply classified as 'body fossils' or 'ichnofossils' (= trace fossils). Dubiofossils have been described by Hofmann (1981), and are not included in the present study. Acritarchs from these strata have also been discussed previously (Baudet *et al.* 1989).

In the following section, synonymies include only Precambrian forms; the occurrence (if any) of Cambrian or younger forms is discussed under 'Remarks'. All type and figured specimens have been deposited in the National Type Collection of Invertebrates and Plants, Geological Survey of Canada (GSC) in Ottawa, Canada.

BODY FOSSILS

Genus BELTANELLA Sprigg, 1947

Type species. Beltanella gilesi Sprigg, 1947.

Beltanella gilesi

Plate 1, fig. 1

For synonymy up to 1987, see Narbonne and Hofmann (1987).

1987 *Beltanella gilesi* Narbonne and Hofmann, pp. 653–654, pl. 73, fig. 6.

1987 *Planomedusites grandis* Gureev, pp. 40–42, fig. 16.

Description. Single incomplete disc preserved in convex hyporelief. Smooth disc 40 mm in diameter with a prominent central tubercle 4.8 mm in diameter; disc surrounded by a flange 5–11 mm wide with irregularly spaced marginal indentations. Poorly preserved, tapering stalk 20 mm wide at its base extending 40 mm beyond the outer edge of the flange.

Remarks. The specimen is strikingly similar to one illustrated by Narbonne and Hofmann (1987, pl. 73, fig. 6) from the Wernecke Mountains of northwestern Canada. *Beltanella* has traditionally been interpreted as a pelagic medusoid (e.g. Sprigg 1947; Harrington and Moore 1956), but Jenkins (1988) recently reinterpreted it as a benthic polyp attached to the sea-bottom by a short stalk. The specimen of *Beltanella* from Sekwi Brook exhibits a poorly preserved stalk which extends outward from the outer margin of the disc, thereby implying that it was above rather than below the disc. As this structure is known from a single specimen, it is uncertain whether or not it is accidental.

Genus CHARNIODISCUS Ford, 1958

Type species. Charniodiscus concentricus Ford, 1958

EXPLANATION OF PLATE 1

Fig. 1. *Beltanella gilesi* Sprigg, hyporelief. Locality 17, Sekwi Brook South, GSC 95895, $\times 1$.

Figs 2 and 6. *Cyclomedusa* sp., hyporelief. 2, locality 3, Sekwi Brook North, GSC 95896, $\times 1$. 6, three specimens that interfered with each other during growth, locality 17, Sekwi Brook South, GSC 95898–95900 (clockwise from top right), $\times 1$.

Fig. 3. Plumose problematicum, epirelief. Locality 3, Sekwi Brook North, GSC 95897, $\times 1.5$.

Fig. 4. *Cyclomedusa plana* Glaessner and Wade, hyporelief. Locality 3, Sekwi Brook North, GSC 95902, $\times 1.5$.

Fig. 5. *Ediacaria* sp., hyporelief. Float, probably from locality 27, Sekwi Brook South, GSC 95903, $\times 0.5$.

Fig. 7. *Charniodiscus*? sp., hyporelief. Locality 30, Majesty Section, GSC 95904, $\times 1$.



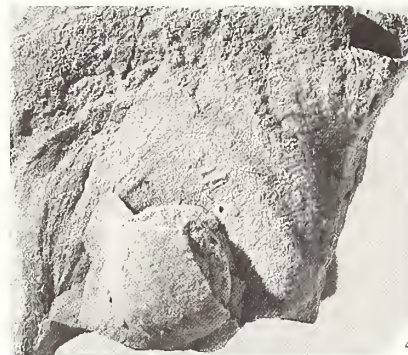
1



2



3



4



5



6



7

Charniodiscus? sp.

Plate 1, fig. 7

Description. Five circular discs preserved in positive hyporelief (0.5–2.5 mm relief). Central tubercle 3–8 mm in diameter surrounded by 3–5 concentric rugae. Disc diameter 26–46 mm (mean = 37.2 mm). Gently tapering stalk, 12–21 mm wide at its base, extending up to 85 mm from the outer margin of the disc.

Remarks. Ford (1958) originally described *Charniodiscus* on the basis of a single concentric disc with an attached stalk, and later (1963) figured the complete specimen with a frond attached to the stalk. Jenkins and Gehling (1978) and Glaessner (1979) subsequently regarded the frond as the most diagnostic part of the fossil. The absence of an attached frond in any of the Sekwi Brook specimens thus far collected precludes more specific identification. Two specimens of the frond of *Charniodiscus* cf. *arboreus* and numerous basal discs of *Charniodiscus?* were described from the Wernecke Mountains by Narbonne and Hofmann (1987, fig. 5c).

Genus CYCLOMEDUSA Sprigg, 1947

Type species. *Cyclomedusa davidi* Sprigg, 1947.

Cyclomedusa plana Glaessner and Wade, 1966

Plate 1, fig. 4

For synonymy to 1987, see Narbonne and Hofmann (1987).

1987 *Cyclomedusa plana* Narbonne and Hofmann, pp. 656–658, pl. 73, fig. 3.

1987 *Glaessneria plana* Gureev, fig. 14.

1987 *Glaessneria imperfecta* Gureev, p. 40, fig. 15.

Description. Two bipartite discs preserved in convex hyporelief. Central cone (5.2 mm relief) or concentrically-ringed disc (< 0.5 mm relief) 5.1–7.1 mm in diameter superimposed on a flat disc approximately 34 mm in diameter. Outer edge of the fossil exhibiting a sharp annulus 0.8–1.2 mm wide and 0.5 mm high. Surface of the outer disc smooth, or marked by very fine radial grooves.

Remarks. The status of *C. plana* is controversial. Until recently, most authors have followed Glaessner and Wade (1966), and regarded it as a species of *Cyclomedusa*. Sun (1986) questioned whether *C. plana* should be included in *Cyclomedusa*, as it is poorly understood and exhibits some significant differences with the type species. Gureev (1987) specifically removed *C. plana* from *Cyclomedusa*, and regarded it as the type species of his new genus *Glaessneria*. Alternatively, Jenkins (1988, 1989) has pointed out that *Cyclomedusa* and other discoid Ediacaran genera have been oversplit, and that there is evidence of intergradation among some of the species of the *Cyclomedusa* plexus and perhaps even among some related genera. Further systematic revision of *Cyclomedusa* is obviously needed, but in the interim we follow Glaessner and Wade (1966) in regarding *C. plana* as a valid species of *Cyclomedusa*.

Most figured specimens of *C. plana*, including material from the Wernecke Mountains (Narbonne and Hofmann 1987) and from Sekwi Brook (e.g. GSC 95901), exhibit a series of concentric wrinkles near the centre of the disc; this presumably represents a conical apex that was folded flat during compaction. One specimen from Sekwi Brook (Pl. 1, fig. 4) resembles two unfigured specimens from South Australia (collected in 1988 and now in the collections of R. J. F. Jenkins) in exhibiting an uncompressed cone at its apex. This implies that the cone was buried in relatively cohesive mud while the flat outer ring rested on the sea floor.

Cyclomedusa plana is a cosmopolitan taxon (Wade 1972), not known from Australia, eastern Europe and western North America (see synonymy in this paper and in Narbonne and Hofmann 1987).

Cyclomedusa sp.

Plate 1, figs 2 and 6; Plate 2, figs 3 and 5

Description. Twenty-one measured specimens and numerous field identifications, all preserved in positive hyporelief. Circular discs 13.4–58.5 mm (mean = 26.2 mm) in diameter with central tubercle, 1.1–7.7 mm; tubercle surrounded by irregularly-spaced concentric markings. Very fine radial ridges locally present (e.g. Pl. 1, fig. 2; Pl. 2, fig. 5). Relief 0.3–3.5 mm, with maximum relief in centre. Specimens deformed laterally where in contact (Pl. 1, fig. 6).

Remarks. Specimens are mostly at the small end of the size range for *Cyclomedusa*, which has a maximum diameter of more than 100 mm (Sun 1986). They closely resemble the specimens illustrated by Wade (1972, pl. 41, fig. 1) as *C. davidi* Sprigg, and like them show evidence that they were originally highly conical. Sun (1986) questioned whether these specimens should be included in *C. davidi* as the radial striations typical of this species are not well developed in Wade's specimens, an objection that applies equally well to the specimens from Sekwi Brook and elsewhere in northwestern Canada (Narbonne and Hofmann 1987). However, the presence of fine radial striae on the bases of *Cyclomedusa* specimens has been attributed by Sun (1986) to composite molding of features on the oral and aboral surfaces. Composite molding is prevalent in the Flinders Ranges but is relatively rare in most other Ediacaran deposits, and it would seem unwise to base a generic difference on a preservational feature. Further systematic revision of *Cyclomedusa* is obviously needed, but in the interim we refer these specimens to *Cyclomedusa* sp.

The interpretation of discoid Ediacaran fossils such as *Cyclomedusa* is uncertain, with various authors regarding them as impressions of pelagic medusae (e.g. Wade 1968; Sun 1986), benthic polyps (e.g. Fedonkin 1985a; Jenkins 1988), sea-pen attachment structures (Jenkins 1989), or burrows similar to those produced by modern actinians (Seilacher 1984). The absence of specimens preserving the oral surface among any of the specimens from northwestern Canada is not consistent with the orientations of medusae stranded at the strand line or in deeper water (cf. Wade 1968). This implies that the aboral surface permanently rested on or in the substrate, and thus that the *Cyclomedusa* organism was benthic. Closely-crowded specimens on the same bedding plane tend to be relatively similar in size (e.g. Hofmann *et al.* 1983, fig. 2A; Narbonne and Hofmann 1987, text-fig. 5a; this study, Pl. 1, fig. 6), and may represent products of a single spatfall. The fact that closely-crowded specimens deform but do not cross-cut each other, and evidence of increasing mutual deformation during growth (Pl. 1, fig. 6), support the interpretation of *Cyclomedusa* sp. as the impression of a sessile benthic organism. Most likely, the prominent central tubercle represents the point where the pelagic larva settled onto the bottom and dug a small pit for attachment to the sea floor. The organism was firm-bodied, and apparently grew out concentrically in the shape of a cone. With the possible exception of the central tubercle there is no evidence of active burrowing; however passive sedimentation of mud around the bases of some of the cones may have resulted in the relatively high relief of some specimens (e.g. Pl. 1, figs 2 and 6). The organism was later buried by a sandy turbidite or storm bed, and was cast by the subsequent collapse of the sand into the space formerly occupied by the organism.

This model implies that *Cyclomedusa* sp. and perhaps other Ediacaran discs with a prominent central tubercle, represent impressions of firm-bodied organisms that were sessile except during their larval stages. The nature of the oral surface remains uncertain, with various authors showing evidence for tentacles (Wade 1972, pl. 41, fig. 2) or stalks (Jenkins 1989, fig. 2E) in some specimens. Elucidation of this is important, as *Cyclomedusa* is one of the most widely recognized Ediacaran fossils.

Genus EDIACARIA Sprigg, 1947

Type species. *Ediacaria flindersi* Sprigg, 1947.

Ediacaria sp.

Plate 1, fig. 5

Description. One nearly complete specimen and one fragment, both preserved in positive hyporelief. Complete specimen a slightly elliptical bipartite disc, 160–170 mm in diameter. Central disc 110–120 mm in diameter, with concentric grooves and discontinuous radial ridges particularly well-developed towards its periphery. Poorly preserved outer flange 25 mm wide, marked by irregular texture and discontinuous radial ridges. Maximum relief of 1.5 mm in the central disc. Possible central circular depression 25 mm in diameter largely covered by sediment.

Remarks. The large size and bipartite to tripartite organization are typical of *Ediacaria*, but the relatively poor quality of preservation does not permit definite comparison with *E. flindersi*, the only named species of this genus. *Ediacaria*, the largest discoid fossil of the Ediacara assemblage, was previously interpreted as a 'medusoid' (Sprigg 1947; Glaessner and Wade 1966) but Fedonkin (1985a) and Jenkins (1988, 1989) have reinterpreted it as an attached polyp.

Genus *EOPORPITA* Wade, 1972

Type species. *Eoporpita medusa* Wade, 1972

Eoporpita sp.

Plate 2, fig. 1; Plate 3, fig. 4

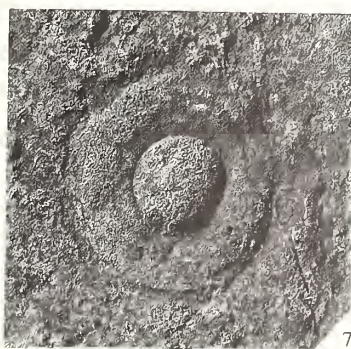
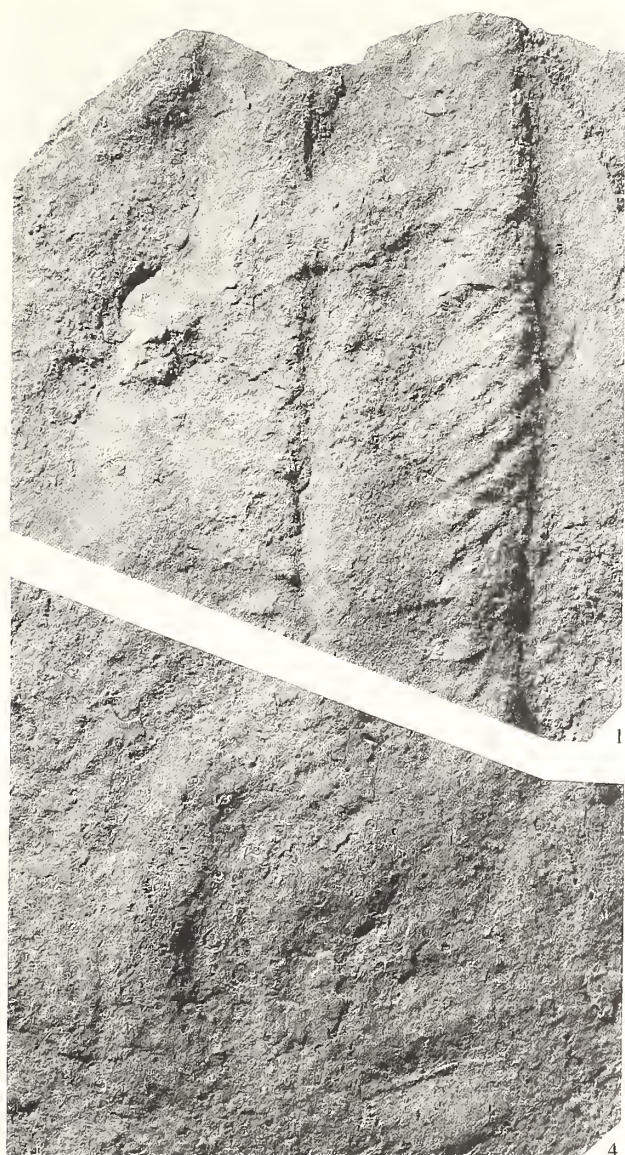
Description. Three discoid specimens preserved in positive hyporelief. Bipartite central cup consisting of a conical knob 4.9–7.1 mm in diameter and 2.1–4.5 mm high surrounded by an upwards-flaring flange 9.2–13.0 mm in diameter and 1.3–1.8 mm high; surface of the flange covered with approximately 12–24 hemispherical to radially elongate pustules 1.5–2.5 mm wide. Flange surrounded by a radiating pattern of approximately twenty-five club-shaped tubes 2.1–4.2 mm wide passing off the pustules and extending outwards to the margin of the fossil. Tubes predominantly straight to slightly sinuous, but locally strongly curved. Total fossil diameter 30–66 mm.

Remarks. The two specimens illustrated in Plate 3, fig. 4 are approximately 25% smaller than the smallest specimens reported by Wade (1972), but the largest specimen is well within the described range of variation of *Eoporpita*. The central cone, radially elongate pustules, and radiating clavate tubes are all diagnostic of *Eoporpita*. However, in contrast with *E. medusa* Wade, which exhibits overlapping whorls of tubes, the Sekwi Brook specimens exhibit only an incipient overlapping near the central zone. For this reason, we refer our material to *Eoporpita* sp.

Wade (1972) originally interpreted *Eoporpita* as a primitive chondrophorian with a chambered float (pneumatophore) and whorls of radiating tentacles, a view supported by most subsequent workers (e.g. Glaessner 1979; Stanley 1986). According to this interpretation, the Sekwi Brook specimens would reflect preservation of the oral surface; the central cone, elongate pustules, and

EXPLANATION OF PLATE 2

- Fig. 1. *Eoporpita* sp., hyporelief. One kilometre north of locality 3, Sekwi Brook North, GSC 95905, $\times 1$.
 Figs 2. *Pteridinium* sp., hyporelief. Locality 18, Sekwi Brook South, GSC 68463, $\times 1$.
 Figs 3 and 5. *Cyclomedusa* sp., hyporelief. Locality 3, Sekwi Brook North. 3, GSC 95907, $\times 1$. 5, GSC 95908, $\times 1$.
 Fig. 4. *Kullingia*? sp., hyporelief. Locality 3, Sekwi Brook North, GSC 95909, $\times 1$.
 Figs 6 and 7. *Medusinites asteroides* (Sprigg), hyporelief. 6, Locality 2, Sekwi Brook North, GSC 95910, $\times 2$.
 7, Locality 3, Sekwi Brook North, GSC 95911, $\times 2$.
 Fig. 8. *Sekwi excentrica* Hofmann, hyporelief. Locality 23, Sekwi Brook South, GSC 95912, $\times 2$.



clavate tubes would respectively represent the gastrozoid, incipient (gonozoid) tentacles and outer (dactylozoid) tentacles. However, experimental taphonomic studies led Norris (1989) to conclude that fossil chondrophorians are very unlikely to preserve a pattern of tentacles similar to that shown by *Eoporpita*. Evidence that the tubes were originally pliable can be seen in GSC 95916, where three of the tubes are deflected against the margin of a large, unidentified discoid fossil, but their original function remains uncertain.

Eoporpita is also known from the Flinders Ranges in Australia and from the White Sea region of the Russian Platform, but had not previously been reported from North America.

Genus KULLINGIA Glaessner in Føyn and Glaessner, 1979

Type species. Kullingia concentrica Glaessner in Føyn and Glaessner, 1979.

Kullingia? sp.

Plate 2, fig. 4

Description. One incomplete disc, partially overlying an indeterminate (?) stalked organism, preserved in convex hyporelief. Disc 160 mm in diameter and less than 1 mm in relief, marked by concentric ridges uniformly spaced 4 mm apart.

Remarks. The specimen is similar in size and morphology to the type species, *K. concentrica*, differing mainly in the wider spacing between concentric ridges. Føyn and Glaessner (1979) pointed out the similarity between the chambered structure of *Kullingia* and the concentrically-chambered float (pneumatophore) of a chondrophorian cnidarian. Alternatively, Seilacher (1984, 1989) suggested that some chambered Ediacaran discs may represent sedentary, benthic 'quasi-autotrophs' that were segmented to facilitate metabolic processes. Close similarity in morphology between Ediacaran, Palaeozoic, and modern chondrophorians supports the view that they are related (Stanley 1986; Narbonne *et al.* 1990).

Genus MEDUSINITES Glaessner and Wade, 1966

Type species. Medusina asteroides Sprigg, 1949.

Medusinites asteroides (Sprigg), 1949

Plate 2, figs 6 and 7

For synonymy up to 1987, see Narbonne and Hofmann (1987).

1987 *Medusinites asteroides* Narbonne and Hofmann, p. 660, pl. 73, figs 7–9

1987 *Medusinites asteroides* Gureev, pp. 30–31, fig. 10.

Description. Nine bipartite discs preserved in convex hyporelief. Smooth outer ring 13.4–24.8 mm (mean 18.7 mm) in diameter and less than 1.5 mm high with an incomplete outer flange 0.2–1.2 mm wide preserved on some specimens. Smooth inner disc 4.2–12.4 mm (mean 7.0 mm) in diameter and 0.5–2.1 mm high separated from outer ring by a sharp annulus. Diameter of the inner disc one quarter of one half of total diameter of the fossil. Fossil surface generally smooth, locally with very faint radial ridges and/or grooves on the outer ring.

Remarks. Specimens closely resemble those described by Glaessner and Wade (1966, pl. 97, figs 1 and 2) from Ediacara and by Narbonne and Hofmann (1987, pl. 73, figs 7–9) from the Wernecke Mountains. Sprigg (1949) and Glaessner and Wade (1966) regarded *Medusinites* as the impression of a medusoid. Alternatively, Fedonkin (1985a) interpreted *Paliella*, a very similar form possibly synonymous with *Medusinites* (Narbonne and Hofmann 1987), as a benthic 'polyp'. The absence

of specimens that preserve the oral surface suggests that *Medusinites* represents the base of a sedentary organism which lived with its mouth facing upwards. This is supported by the relatively high relief of some specimens, which implies that their bases were already buried in the mud at the time of sand deposition.

Genus *PTERIDINIUM* Gürich, 1933

Type species. Pteridinium simplex Gürich, 1933.

Pteridinium sp.

Plate 2, fig. 2

Description. One specimen figured by Aitken (1989a, fig. 6A) but not previously described; the scale bar on Aitken's figure is incorrect, and should read 3.75 cm. Specimen at least 92 mm long (incomplete at both ends), 60–62 mm wide, and with 4.5 mm of relief. Straight, smooth ribs 3.5–4 mm wide passing laterally from median furrow (V-angle = 100–120°) to the margin of the fossil. No evidence of a third vane.

Remarks. Pflug (1970) interpreted *Pteridinium* as a three-vaaned, leaf-like structure. Distortion of these flexible organisms led to the wide range in morphology evident in *Pteridinium* (cf. Richter 1955; Glaessner and Wade 1966; Pflug 1970; Fedonkin 1981), a problem which hinders the recognition of species and comparisons with related forms such as *Inkrylovia*. *Pteridinium* was a cosmopolitan taxon that occurred over a broad bathymetric range (Gibson *et al.* 1984). The specimen from Sekwi Brook South in the first Ediacaran body fossil reported from deep-water carbonates.

Genus *SEKWIA* Hofmann, 1981

Type species. Sekwia excentrica Hofmann, 1981.

Sekwia excentrica Hofmann, 1981

Plate 2, fig. 8

1981 *Sekwia excentrica* Hofmann, pp. 305–307, fig. 4A–G.

Remarks. *Sekwia* was originally defined by Hofmann (1981) on the basis of twenty-four specimens collected from strata now assigned to the middle part of the Blueflower Formation at Sekwi Brook South. Our fieldwork in 1988 resulted in the discovery of two additional specimens from the same bed. Both specimens are well within the range of variation described by Hofmann (1981).

Sekwia excentrica is similar in size and eccentricity to the laterally deformed specimens of *Cyclomedusa* sp. (Pl. 1, fig. 7; Wade 1972, pl. 41, fig. 1) and *Sekwia kaptarenkoe* Gureev, 1987, but exhibits much lower relief and apparently lacks a central tubercle. One high-relief specimen questionably identified as *Sekwia* by Hofmann (1981, fig. 4H) was later referred to *Beltanelliformis* by Narbonne and Hofmann (1987). Re-examination of this specimen by the present authors suggests that it represents an indeterminate fossil that has been badly deformed by loading, and cannot definitely be ascribed to either of these genera.

Sekwia probably represents the impression of a highly conical cnidarian (Hofmann 1981), most likely a 'polyp' similar in some respects to *Cyclomedusa* sp., that was flattened and deformed laterally during burial.

Plumose Problematicum

Plate 1, fig. 3

Description. One incomplete specimen preserved in negative hyporelief. Preserved length 51 mm, with a

maximum relief of 2.3 mm. Specimen petaloid, with a sharp outer margin. Plumose arrangement of sharp ridges 1–2.5 mm wide and up to 1.4 mm high extending the length of the specimen.

Remarks. The specimen superficially resembles tectonic features such as plumose fractures, but this is ruled out by the presence of a thin carbonaceous lamella that evenly covers the entire bedding surface, including the sides and tops of the fine ridges. This indicates that they represent very sharp folds of the bedding surface (prelithification) rather than tectonic fractures of the rock surface (postlithification). The presence of a sharp outer margin is also atypical of plumose fractures. Preservation of the structure in negative hyporelief, and the occurrence of undeformed specimens of indeterminate discoid megafossils preserved in positive hyporelief elsewhere on the same slab (GSC 95906), both imply that the structure does not represent a load mark, a pattern of rill marks, or some other inorganic sedimentary structure.

The specimen resembles the oral surface of a single lobe of *Inaria karli* Gehling, 1988 in size, preservation in negative hyporelief, and the plumose arrangement of longitudinal ridges, but differs in exhibiting a single rather than double border and in several other respects. Broad comparisons can also be made with *Lomosovis* Fedonkin, which, however, is parallel-sided rather than petaloid and also differs in the pattern of ridge development. The range of morphology of the Plumose Problematicum is unknown, as it is presently known only from a single, fragmentary specimen.

The Plumose Problematicum probably represents a bag-shaped organism that was folded longitudinally during burial.

ICHNOFOSSILS

Ichnogenus AULICHNITES Fenton and Fenton, 1937

Type ichnospecies. *Aulichnites parkerensis* Fenton and Fenton, 1937.

Aulichnites ichnosp.

Plate 3, figs 1 and 3

Description. Ten specimens preserved in positive relief. Unbranched, horizontal, sinuous to irregularly meandering, 10–11 mm wide bilobate trails; one specimen passing laterally into a trilobate trail. Smooth lobes separated by a median furrow 2–3 mm wide. Cross-sectional shape indeterminate, despite sectioning.

Remarks. Specimens are approximately twice as large as those figured by Fedonkin (1980, pl. 1, figs 3–5; 1985c, pl. 26, figs 1 and 8) from the Vendian of the White Sea area, but are otherwise similar. They are similar to the type species, *A. parkerensis*, in size and overall morphology, but differ in the absence of curved striae on the surface of the lobes. Some of the type specimens of *A. parkerensis*

EXPLANATION OF PLATE 3

- Figs 1 and 3. *Aulichnites* sp., epirelief. Locality 13, Sekwi Brook North. 1, GSC 95913, $\times 1$. 3, GSC 95914, $\times 1$.
 Fig. 2. *Helminthopsis abeli* Książkiewicz, 1977, hyporelief. Locality 26, Sekwi Brook South, GSC 95915, $\times 0.75$.
 Fig. 4. *Eoporpita* sp., hyporelief. Locality 3, Sekwi Brook North, GSC 95916 (lower left), GSC 95917 (upper right), $\times 1$.
 Fig. 5. *Planolites montanus* Richter, hyporelief. Locality 30, Majesty Section, GSC 95918, $\times 1$.
 Figs 6–8. *Palaeophycus tubularis* Hall. 6, hyporelief, locality 13, Sekwi Brook North, GSC 95919, $\times 1$. 7, hyporelief, locality 30, Majesty Section, GSC 95920, $\times 1$. 8, cross-section of 7 showing thin clay lining and partial collapse.
 Fig. 9. *Neonereites*? sp. and *Planolites montanus*, hyporelief. Locality 11, Sekwi Brook North, GSC 95921 and 95922, $\times 1.5$.



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exhibit a unilobed lower surface (Hakes 1977), a feature not determinable on the present material. These preservational features preclude identification of the Sekwi Brook specimens to the ichnospecies level.

Aulichnites is generally interpreted as the grazing trail of a gastropod (Fenton and Fenton 1937; Häntzschel 1975; Howard and Frey 1984) or similar organism. Yochelson and Schindel (1978) doubted this interpretation, but did not offer specific reasons for their view. *Aulichnites* also ranges throughout the Phanerozoic (Häntzschel 1975). It occurs most commonly in shallow marine deposits (Hakes 1977), but is also found in deep-water turbidites (Hill 1981).

Ichnogenus HELMINTHOIDA Schafhäutl, 1851

Type ichnospecies. *Helminthoida labyrinthica* Heer, 1865.

Helminthoida ichnosp.

Plate 4, fig. 1

Description. One specimen preserved in part and counterpart, and a second uncollectable specimen studied in the field. Unbranched, unlined, horizontal meandering burrows 2.1–2.9 mm wide, with smooth surface and fill similar to host lithology. Meanders increasing in amplitude distally from 100–150 mm; wavelength 40–60 mm. Adjacent burrow segments parallel to sub-parallel.

Remarks. *Helminthoida* is a regularly meandering, hemicylindrical trace that shows a strong tendency towards development of parallel meanders (Häntzschel 1975; Książkiewicz 1977). As such, it can readily be distinguished from *Taphrhelminthoida* Książkiewicz (which is bilobate) and *Helminthopsis* Heer (which is less regularly meandering). The specimens of *Helminthoida* from Sekwi Brook display the meandering habit diagnostic of the ichnogenus, but are considerably larger and exhibit more open meanders than most Phanerozoic specimens (but see the Early Cambrian specimens of *H. miocenica* in Crimes and Anderson 1985, figs 7.3–7.5). Seilacher (1974, 1977) has documented similar trends in the evolution of other meandering trace fossils such as *Nereites*, and has related it to a gradual decline in body size and increase in behavioural complexity in deep-sea environments throughout the Phanerozoic.

Helminthoida is a characteristic element of Cretaceous-Tertiary flysch deposits (e.g. Seilacher, 1964; Książkiewicz 1970, 1977; Crimes 1977) and also occurs in Recent deep-sea sediments (Chamberlain 1975). It has been reported from Ordovician and Silurian flysch (Pickerill 1980, 1981) and from Early Cambrian storm deposits of eastern Newfoundland (Crimes and Anderson 1985). Glaessner (1969) figured complexly meandering burrows from Ediacara under the name 'Form C'; these have been compared with *Helminthoida* by Crimes (1987) and are also quite similar to *Yelovichnus gracilis* Fedonkin, 1985c from the Vendian of the White Sea area. Fedonkin (1985c) has also figured specimens of *Helminthoida* ichnosp. from the same strata.

EXPLANATION OF PLATE 4

Fig. 1. *Helminthoida* sp., hyporelief. Locality 10, Sekwi Brook North, GSC 95923, $\times 0.5$.

Figs 2 and 3. *Helminthoidichnites tenuis* Fitch, epirelief. 2, locality 6, Sekwi Brook North, GSC 95924, $\times 0.5$. 3, locality 19, Sekwi Brook South, GSC 95925, $\times 0.5$.

Fig. 4. *Helminthopsis?* sp., epirelief. Locality 11, Sekwi Brook North, GSC 95926, $\times 0.5$.

Figs 5 and 6. *Helminthopsis irregularis* (Schafhäutl), hyporelief. Locality 26, Sekwi Brook South. 5, GSC 95927, 1. 6, GSC 95928, $\times 0.75$.



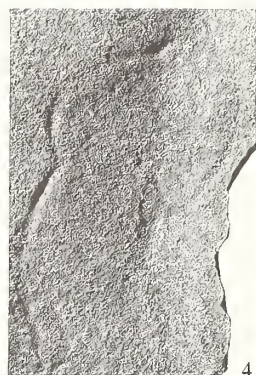
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Ichnogenus *HELMINTHOIDICHNITES* Fitch, 1850

Type ichnospecies. *Helminthoidichnites tenuis* Fitch, 1850

Helminthoidichnites tenuis

Plate 4, figs 2 and 3

- 1969 'Form B' Glaessner, p. 381, fig. 5B.
- ?1969 'Form E' Glaessner, p. 382, fig. 5F.
- 1976 'crawling trails' Palij, pl. 26, figs 1 and 2.
- 1979 'crawling trails, first variety' Palij *et al.*, p. 77, pl. 53, figs 2 and 4.
- 1981 *Gordia* sp. Hofmann, p. 307, fig. 5B.
- 1981 *Gordia*? sp. Hofmann, p. 307, fig. 5D.
- 1983 *Gordia* sp. Fritz *et al.*, pl. 44.1, fig. 3.
- 1985 *Gordia* sp. Crimes and Anderson, p. 321, fig. 5.8.
- 1985c *Gordia* sp. Fedonkin, pl. 23, fig. 1.
- 1987 *Gordia marina* Narbonne and Hofmann, pp. 668–670, text-fig. 10a
- 1989a *Planolites* sp. Aitken, fig. 6C.
- 1989 *Planolites beverleyensis* Gibson, p. 5, figs 3.8 and 4.1.

Description. Numerous specimens (47 measured) preserved in both positive and negative relief on the tops and soles of beds. Irregularly sinuous to meandering, smooth, unlined, cylindrical burrows 1.1–3.3 mm (mean = 2.1 mm) in diameter; diameter constant within a single specimen. Burrows commonly crossing adjacent specimens, and rarely (three examples) crossing previously constructed portions of the same specimen. Specimens preserved in negative epirelief with narrow levées. Specimens preserved in positive relief with fill similar to host lithology, and flanked by narrow grooves. True branching absent, but offset of crossing specimens commonly producing pseudobranches.

Remarks. *Helminthoidichnites* is herein used in the sense of Hofmann and Patel (1989) for irregularly sinuous to meandering burrows with random crossings of the same and adjacent burrows. As such, it differs from *Gordia* Emmons, 1844 which exhibits long parallel limbs with numerous over-crossings, and from *Helminthopsis* Heer, 1877 which is irregularly meandering but avoids level crossings of the same or adjacent burrows. The Sekwi Brook specimens are most similar to material from Ediacara described by Glaessner (1969) as 'Form B', and to *Gordia* sp. from the late Precambrian of the Burin Peninsula, Newfoundland (Crimes and Anderson 1985). Specific points of similarity include the size, presence of narrow levées, development of pseudobranches, and the tendency of burrows commonly to cross adjacent burrows but only rarely to cross themselves.

Helminthoidichnites is common in the Ediacaran, where it previously has been referred to *Gordia* or *Planolites* (see synonymy), and also ranges throughout the Phanerozoic (Hofmann and Patel 1989). It is eurybathic, and probably represents the crawling or feeding trail of a vermiform organism.

Ichnogenus *HELMINTHOPSIS* Heer, 1877

Type ichnospecies. *Helminthopsis magna* Heer, 1877 (but see Książkiewicz 1977, p. 116).

Helminthopsis abeli Książkiewicz, 1977

Plate 3, fig. 2

Description. Three specimens preserved in positive hyporelief. Smooth, unbranched, unlined, hemicylindrical burrows 6.0–6.3 mm in diameter, with burrow-fill similar to host lithology. Burrows loosely winding, with a tendency to meandering.

Remarks. The specimens closely conform in size and morphology to those illustrated by Książkiewicz (1977, pl. 12, fig. 5; text-fig. 21a–h). *H. abeli* ranges throughout the Phanerozoic, in rocks of both shallow-marine (e.g. Crimes and Anderson 1985) and especially deep-sea (e.g. Książkiewicz 1977) aspect. It had not previously been reported from the Precambrian.

Helminthopsis is an irregularly meandering burrow that avoids level-crossings (Książkiewicz 1977). The ichnogenus has been reported from the Precambrian of the Cassiar Mountains, northwestern Canada (Fritz and Crimes 1985) and the Carolina Slate Belt of the southeastern USA (Gibson 1989), and also ranges throughout the Phanerozoic (Häntzschel 1975). *Helminthopsis* is eurybathic, but is most commonly reported from deep-water flysch deposits (Pickerill 1981). It represents the feeding or grazing burrow of a vermiform organism, most likely an annelid (Książkiewicz 1977).

Helminthopsis irregularis (Schafhäutl), 1851

Plate 4, figs 5 and 6

Description: Numerous specimens preserved in positive hyporelief on eleven slabs. Burrows ranging from irregularly winding to tightly meandering with parallel arms and second-order windings, even within the same specimen. Burrows unbranched and unlined, with fill similar to host lithology, predominantly smooth but with local transverse markings. Burrow diameter 1.4–3.1 mm, with diameter constant within any single specimen. Cross-overs of the same or adjacent burrows absent.

Remarks. This ichnospecies was originally assigned to *Helminthoida* Schafhäutl. Książkiewicz (1977) regarded it as a very regular version of *Helminthopsis* rather than an irregular version of *Helminthoida*, a view with which we concur. *Helminthopsis irregularis* exhibits two behavioural approaches to avoid level-crossings (Pl. 4, figs 5 and 6). The most common approach is to cross at a stratigraphically higher or lower level than the previous burrow; this avoids crossings, but requires that the feeding organism leave the organic-rich bedding plane briefly. A less common, but more efficient method is the local development of subparallel meanders to avoid crossing over its own or an adjacent burrow. This represents a primitive version of *phobotaxis* (sensu Richter 1928), which characterizes meandering burrows in Phanerozoic deep-sea deposits (Seilacher 1967, 1974; Raup and Seilacher 1968).

H. irregularis has previously been described only from Mesozoic and Tertiary, deep-water flysch deposits (Książkiewicz 1977). Paczeńska (1988) listed, but has not yet figured or described, a possible specimen from the upper Proterozoic Lublin Formation of Poland.

Helminthopsis? ichnosp.

Plate 4, fig. 4

Description. One specimen preserved in negative epirelief. Horizontal burrow 2 mm in diameter consisting of a series of connected arcuate loops. Burrow flanked by narrow levées.

Remarks. The single specimen is most similar to one illustrated by Gibson (1989) from the deep-water Carolina Slate Belt of the southeastern U.S.A. Broad comparisons can also be made with *Gordia arcuata* Książkiewicz, 1977, but *Helminthopsis* sp. is considerably less arcuate with turnings confined to the horizontal plane.

Ichnogenus *LOCKEIA* James, 1879

Type ichnospecies. *Lockeia siliquaria* James, 1879.



TEXT-FIG. 7. A–C, *Torrowangea rosei* Webby, hyporelief; A, locality 29, Majesty Section, GSC 95929, $\times 1$; B, locality 15, Sekwi Brook North, GSC 95930, $\times 1$; C, locality 29, Majesty Section, GSC 95931, $\times 1$. D, Knotted circular burrow, hyporelief. Locality 11, Sekwi Brook North, GSC 95932, $\times 0.5$. E–H, *Lockeia ichnosp.*, locality 13, Sekwi Brook North; E–G, hyporelief, GSC 95933–95937, $\times 2$; H, photomicrograph cross-section, GSC 95938, $\times 5$.

Lockeia ichnosp.

Text-fig. 7E-H

Description. Eight specimens preserved in positive hyporelief. Oblong bodies 4.3–5.6 mm (mean = 5.2 mm) long and 2.4–2.9 mm (mean = 2.7 mm) wide, with a constant length/width ratio of approximately 2:1. Specimens smooth and almond-shaped, with one rounded and one pointed end. Maximum relief 2.2 mm; burrow-fill structureless, and similar in composition to the overlying quartzarenite bed. Sandstone sole sharply upturned in the immediate vicinity of the burrow.

Remarks. This ichnogenus is referred to under the name *Pelecypodichnus* Seilacher by many workers, but we agree with Osgood (1970), Häntzschel (1975) and Maples and West (1989) that *Lockeia* is a valid name and the subjective senior synonym of *Pelecypodichnus*. The specimens from Sekwi Brook are similar to *L. amygdaloides* (Seilacher) in exhibiting an almond-shaped cross-section and a consistent 2:1 length/width ratio, but lack the keel present on some specimens of *L. amygdaloides*.

Based on its symmetry and comparisons with the burrows of modern bivalves, Seilacher (1953) concluded that *Lockeia* ('*Pelecypodichnus*') represents the resting burrow of a bivalve. Seilacher's view has been supported by virtually all subsequent workers (e.g. Osgood 1970; Eager 1974; Hakes 1976, 1977; Bromley and Asgaard 1979; Thoms and Berg 1985; Wright and Benton 1987), many of whom suggested specific bivalve genera as the originators of the *Lockeia* in their sections. The Sekwi Brook specimens of *Lockeia* exhibit typical bivalve symmetry, with a single plane of mirror symmetry that passes longitudinally through the structure. Another feature consistent with a bivalve origin is the upturning of the sole of the bed in the immediate vicinity of the burrow, and the associated upward pinch of clay drapes around the burrow (Text-fig. 7H). This feature has been described from Phanerozoic specimens of *Lockeia amygdaloides* (e.g. Bromley and Asgaard 1979, fig. 5B), and implies that the mode of burrowing was bivalve-like, and consisted of probing and penetration rather than excavation (Pojeta 1987).

Bivalves are the only extant organisms that exhibit both a cross-sectional shape and a mode of burrowing consistent with the Sekwi Brook specimens of *Lockeia*. However, the oldest confirmed bivalve body fossils are Early Cambrian (Pojeta *et al.* 1973; Pojeta 1985; Runnegar 1985). The presence of *Lockeia* in the Ediacaran implies either that very thin-shelled/poorly calcified bivalves evolved in the Late Precambrian, or that *Lockeia* could also be constructed by a now extinct group of organisms similar to bivalves in some morphological and behavioural aspects.

Lockeia is a facies-crossing ichnogenus that is known from a wide range of non-marine (e.g. Bromley and Asgaard 1979) and shallow to deep marine (e.g. Crimes 1977, table 4) settings.

Ichnogenus NEONEREITES Seilacher, 1960

Type ichnospecies. *Neonereites biserialis* Seilacher, 1960.

Neonereites? ichnosp.

Plate 3, fig. 9

Description. Two specimens preserved in positive hyporelief. Each specimen comprising a gently curved, uniserial string of hemispheres, 0.4–0.7 mm in relief and composed of fine sandstone similar to host lithology; adjacent hemispheres in contact. Hemispheres progressively increasing in size distally. Larger specimen 16.0 mm long, consisting of 7 hemispheres 1.2–3.5 mm in diameter; smaller specimen 8.1 mm long, consisting of 4 hemispheres 1.7–2.7 mm in diameter.

Remarks. The specimens are most similar to *Neonereites uniserialis* Seilacher, but differ in that hemispheres progressively increase in size along the chain. No similar forms of *Neonereites* have previously been described.

Neonereites is commonly reported from Ediacaran strata (Text-fig. 6), and also ranges throughout the Phanerozoic (Häntzschel 1975). It is a facies-crossing form (Seilacher 1964; Crimes 1977) which represents the feeding burrow of a vagile vermiform organism, probably an annelid (Hakes 1976).

Ichnogenus PALAEOPHYCUS Hall, 1847

Type ichnospecies. Palaeophycus tubularis Hall, 1847.

Palaeophycus tubularis Hall, 1847

Plate 3, figs 6–8

Description. Thirty-four specimens preserved in convex hyporelief and full relief. Straight, curved, to gently sinuous, horizontal, predominantly unbranched, hemicylindrical to cylindrical burrows, 3.7–7.1 mm (mean = 5.8 mm) in diameter. Preserved length up to 140 mm. Burrows smooth-walled and very thinly lined with clay, locally partially collapsed, and with fill similar to host lithology.

Remarks. The taxonomy of *Palaeophycus* has been reviewed by Pemberton and Frey (1982), who distinguished it from the similar ichnogenus *Planolites* Nicholson by the presence of a burrow-lining fill similar to the host lithology, and local evidence of partial burrow collapse. These features reflect passive filling of originally open burrow systems constructed by suspension-feeding or predaceous organisms, predominantly annelids (Pemberton and Frey 1982). *Palaeophycus* is common in Phanerozoic strata, where it occurs in virtually all sedimentary facies (Pemberton and Frey 1982). It is commonly reported in compilations as ranging in age from 'Precambrian to Recent' (e.g. Häntzschel 1975), but the only primary report of Precambrian *Palaeophycus* known to us is from the Risky Formation of the Wernecke Mountains (Nowlan *et al.*, 1985). The second variety of 'crawling traces' described by Palić *et al.* (1979, pp. 77–78, pl. 53, fig. 5; pl. 54, fig. 1) from the Vendian of Podolia is broadly similar, but further details of the nature of the burrow fill and the presence or absence of a burrow lining are necessary to determine whether it represents *Palaeophycus* or *Planolites*.

Ichnogenus PLANOLITES Nicholson, 1873

Type ichnospecies. Planolites vulgaris Nicholson and Hinde, 1875.

Planolites montanus Richter, 1937

Plate 3, figs 5 and 9

- 1970 'hypichnial and exichnial casts' Banks, p. 26, pl. 1*b,d*.
- 1970 'trails' Webby, pp. 87–88, fig. 3*B–D*, ?fig. 4*a–b*.
- 1972*a* 'threadlike trails' Germs, p. 208, pl. 26, figs 5 and 7, pl. 27, fig. 1.
- 1972*b* 'threadlike trails' Germs, p. 866, pl. 1, figs 5 and 7, pl. 2, fig. 1.
- 1973 'hypichnial and endichnial burrows' Banks, p. 4, fig. 4*a*.
- 1977 *Planolites* sp. Fedonkin, p. 184, pl. 2*d*.
- 1979 'crawling traces, third variety' Palić *et al.*, pp. 77–78, pl. 54, fig. 2.
- 1979 *Planolites* cf. *serpens* Palić *et al.*, p. 73, pl. 42, fig. 6.
- 1984 *Planolites* sp. Glaessner, p. 70, fig. 2/7.
- 1985*c* *Planolites* cf. *serpens* Fedonkin, pl. 28, figs 3 and 6.
- 1987 *Planolites montanus* Narbonne and Hofmann, pp. 670–671, text-fig. 10*b,d*.
- 1989 *Planolites montanus* Gibson, p. 5, fig. 4.1.

Description. Numerous specimens preserved in convex hyporelief and full relief. Burrows cylindrical, unbranched and unlined, and with structureless fill dissimilar to host lithology. Burrows highly sinuous and undulatory, occurring on bedding surfaces as small knobs and as discontinuous burrow segments typically less than 5 mm long (but ranging up to 55 mm long). Burrow diameter 0.3–1.7 mm (mean = 0.8 mm; $n = 120$).

Remarks. The taxonomy of *Planolites* was reviewed by Pemberton and Frey (1982), who recognized only three valid ichnospecies from among the thirty-three formally defined forms; several new ichnospecies have been named subsequently. The Mackenzie Mountain specimens fall within the diagnosis of *P. montanus* as 'relatively small, curved to contorted burrows' (Pemberton and Frey 1982, p. 870). *Planolites* is a eurybathic ichnogenus that could be produced by a wide variety of vermiform organisms (Alpert 1975; Pemberton and Frey 1982).

Planolites ranges in age from Ediacaran to Recent (Häntzschel 1975). *P. montanus* occurs throughout the Phanerozoic (Pemberton and Frey 1982, pp. 869–870) and is perhaps the most widely distributed Ediacaran ichnospecies (see synonymy).

Ichnogenus TORROWANGEA Webby, 1970

Type ichnospecies. *Torrowangea rosei* Webby, 1970.

Torrowangea rosei Webby, 1970

Text-fig. 7A–C

- 1981 *Torrowangea* sp. Hofmann, p. 309, fig. 5C.
- 1985 *Torrowangea rosei* Paczeńska, pl. 1, figs 1, 2, 5.
- 1986 *Torrowangea rosei* Paczeńska, p. 35, pl. 1, figs 1 and 4
- 1987 *Torrowangea* sp. Narbonne *et al.*, fig. 6C.
- 1989a *Torrowangea* sp. Aitken, fig. 6B.

Description. Numerous specimens preserved in positive hyporelief and rarely in negative epirelief. Sinuous to irregularly meandering, horizontal burrows. Burrows unbranched and unlined; cross-overs of the same or adjacent individuals occurring commonly, in some instances forming figure-8 pattern. Burrows 0.8–2.7 mm (mean = 1.8 mm; $n = 160$), with irregularly-spaced transverse constrictions resulting in a marked 'pinch-and-swell' appearance. Burrow-fill slightly coarser and better sorted than host lithology.

Remarks. *Torrowangea* sp. was described from the Sekwi Brook South section by Hofmann (1981) on the basis of relatively few specimens. Our analysis of several hundred specimens confirms Hofmann's generic identification, and further suggests that the material can be referred to *T. rosei*. Irregularly meandering and crossing specimens similar to Webby's (1970, fig. 18C) holotype occur rarely (Text-fig. 7A, C), but most specimens are sinuous (Text-fig. 7B) and are best compared with two of the paratypes figured by Webby (1970, fig. 18A, B) and with the specimens illustrated by Hofmann (1981) and Paczeńska (1985, 1986).

The present specimens slightly extend the range of burrow diameters for *Torrowangea* in both directions, but the mean is well within the range of the type material. The marked 'pinch-and-swell' appearance of *Torrowangea* was interpreted by Webby (1970) as a backfill structure, but this is not consistent with the apparent absence of internal structure in longitudinal thin sections of the Mackenzie Mountain specimens. Most likely, it reflects peristalsis.

Torrowangea was originally described from the Lintiss Vale Formation of New South Wales, Australia (Webby 1970). The age of this unit is controversial, with some authors favouring a latest Precambrian (probably Kotlin-equivalent) age and others favouring an earliest Cambrian (probably Rovno-equivalent) age (see review in Webby 1984). Narbonne and Myrow (1988) and Walter *et al.* (in press) believed that the presence of *Phycodes*? and other complex burrows favoured the latter

view. *Torrowangea* has been described from undoubted Precambrian strata (e.g. Paczeńska 1985, 1986), and from subtrilobite Lower Cambrian deposits (e.g. Aceñolaza and Durand 1973). Pemberton and Frey (1982) tentatively referred ?*Planolites octichnus* Chamberlain, 1971 from the Carboniferous of Oklahoma to *Torrowangea*; our examination of Chamberlain's specimens indicated that the pattern of meandering is similar but that the irregular transverse constrictions diagnostic of *Torrowangea* are not present.

Torrowangea represents the feeding burrow of a worm-like organism, probably an annelid. It occurs in both shallow-water and deep-water deposits, and is most common in fine-grained, muddy sandstones. In the Sekwi Brook area, specimens also occur in ribbon-bedded lime mudstone.

Knotted Burrow

Text-fig. 7D

Description. Single specimen preserved in positive hyporelief. Unlined(?) hemicylindrical burrow 3.1 mm in diameter forming an irregular circle 59–79 mm in diameter, and forming a crude 'knot' at the point of overcrossing. Three arcuate burrows radiating outwards more than 100 mm. Burrow fill similar to host lithology.

Remarks. The overall structure is unlike any known to us. The central circle is somewhat larger and less regular than *Circulichnis montanus* Vyalov, 1971, but is otherwise similar. *Circulichnis* ranges throughout the Phanerozoic (Fillion and Pickerill 1984), and is also figured under the name *Gordia arcuata*? from the late Precambrian of the Carolina Slate Belt (Gibson 1989, fig. 3.1). It is eurybathic, but is most commonly reported from deep-water settings (Fillion and Pickerill 1984).

Similarity between the diameters of the circle and the branches, termination of all the branches at the circle, and the extreme scarcity of arcuate burrows of similar size elsewhere in the Blueflower Formation, implies that central circular burrow and the radiating arcuate burrows are related. The arcuate burrows may represent different activity by the same species or even organism, or (less likely) may represent branches that pass off the circular knotted burrow at a higher stratigraphic level and descend rapidly to the level of the bedding surface.

CONCLUSIONS

1. Ediacaran fossils occur sporadically throughout approximately one kilometre of deep-water strata, encompassing the upper Sheepbed Formation to the top of the Blueflower Formation, in the Sekwi Brook area of northwestern Canada. At least eleven body fossil species and twelve ichnospecies are present in this interval.

2. Ediacaran megafossils at Sekwi Brook comprise mainly sessile, benthic polypoid and frond-like organisms along with a single, presumably pelagic, chondrophorian. The occurrence of a predominantly *in situ* benthic fauna in muddy slope deposits below storm wave-base is not consistent with the hypothesis that these taxa functioned exclusively as photoautotrophs.

3. The Sekwi Brook megafossil assemblage is broadly similar to that reported from coeval shallow shelf deposits in the Wernecke Mountains, Flinders Ranges and Russian Platform, but apparently lacks the (?)actinian impression *Beltanelliformis* which is abundant in Ediacaran shallow shelf deposits. Similarity of Ediacaran assemblages in shelf and slope settings implies that the organisms had broad palaeoenvironmental ranges, and enhances their correlation potential.

4. The occurrence of a relatively diverse trace fossil assemblage at Sekwi Brook implies that the initial radiation of infaunal organisms extended into slope settings. The ichnocoenoses includes irregularly and regularly meandering burrows, and may represent a primitive version of the *Nereites* ichnofacies, which characterizes deep-water Phanerozoic deposits.

Acknowledgements. We gratefully acknowledge excellent field assistance by Paul Fejer and Lascelles Gayle, and the skill of our Okanagan helicopter pilots Lois Hill, Tony Duckworth and Ray Portlock. Critical comments by M. M. Anderson, M. A. Fedonkin, H. J. Hofmann, R. J. F. Jenkins and R. K. Pickerill greatly improved the manuscript. Olga Iljewiwn translated critical articles, and Clinton Cowan, Steve Forrester, John Milne, and Ela Mazur assisted with drafting and photography. T. E. Bolton (Geological Survey of Canada), R. J. F. Jenkins (University of Adelaide), N. Pledge (South Australia Museum), and K. Westphal (University of Wisconsin, Madison) provided access to relevant type specimens. Narbonne also acknowledges financial assistance from the Natural Sciences and Engineering Research Council of Canada (NSERC Grant A2648) and the Queen's University Advisory Research Committee. This is Geological Survey of Canada Publication No. 28089.

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Typescript received 15 August 1989

Revised typescript received 19 January 1990

A NEW SPECIES OF LATE CRETACEOUS WOOD-BORING BIVALVE FROM NEW ZEALAND

by J. S. CRAMPTON

ABSTRACT. A new species of late Campanian or Maastrichtian (Late Cretaceous) pholadid bivalve, *Pholadidea* (*Hatasia*) *wiffenae*, is described from shallow marine transgressive Maungataniwha Sandstone, northwestern Hawkes Bay, New Zealand. It represents the earliest confirmed record for both genus and subgenus. The new species is known from exceptionally well-preserved material, which permits detailed knowledge of external morphology, including all accessory plates, and to a lesser degree, internal morphology. It is assigned to *Pholadidea* (*Hatasia*) based largely on the nature of accessory plates. In life-habit and some details of morphology, however, *P. (H.) wiffenae* resembles *Opertochasma* and *Martesia*, and may be an evolutionary intermediate between Cretaceous *Opertochasma* and early Tertiary *Pholadidea* and *Martesia*. The present record highlights the need for a comprehensive systematic review of Mesozoic pholadids.

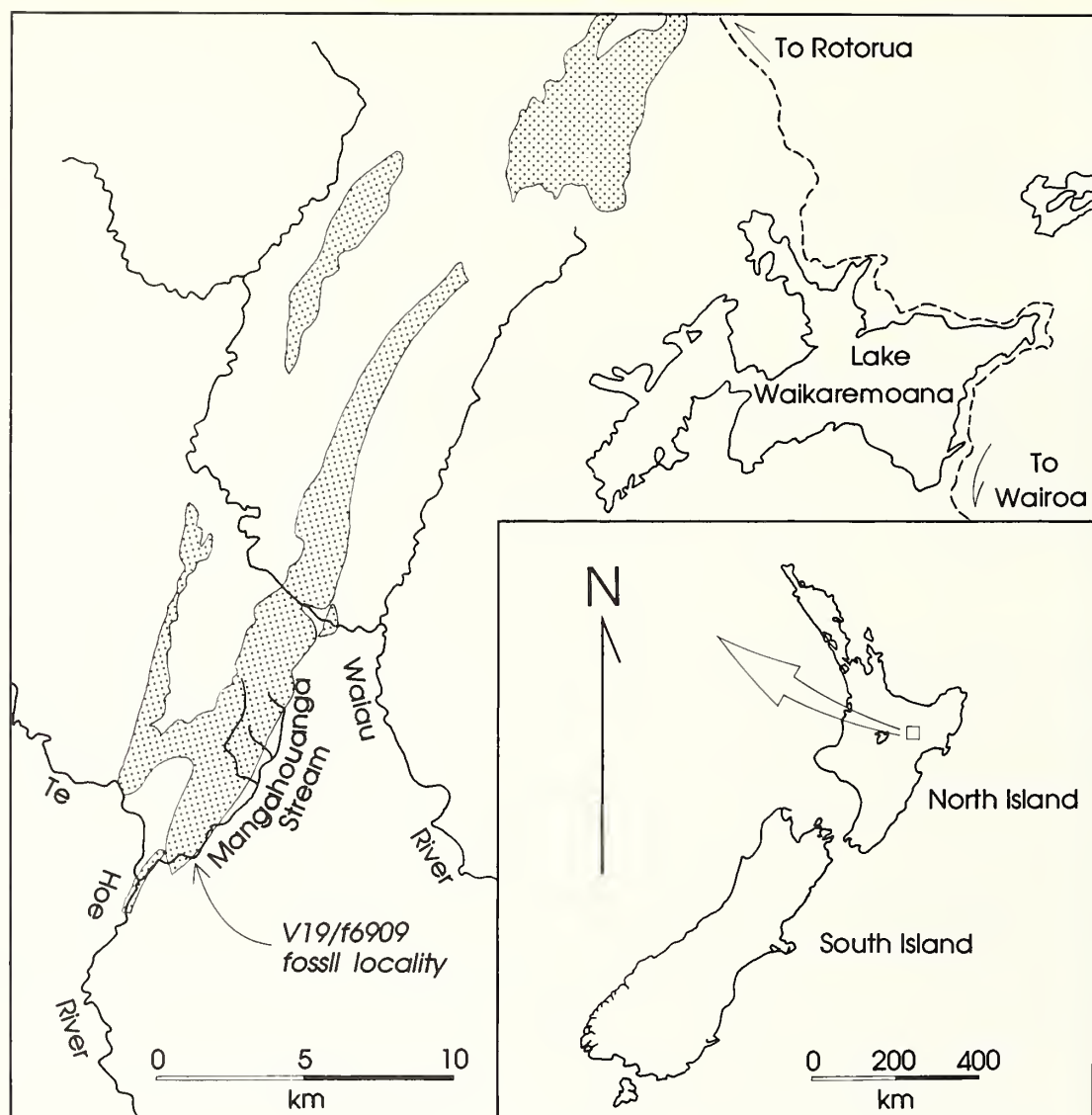
THE late Cretaceous Maungataniwha Sandstone (Moore 1986), outcropping west and southwest of Lake Waikaremoana, northwestern Hawkes Bay, New Zealand (Text-fig. 1), contains the most diverse faunas of this age known from New Zealand. Included are terrestrial and freshwater invertebrates (Craw and Watt 1987; Moore *et al.* 1988), marine invertebrates (Glaessner 1980; Wiffen 1980; Crampton 1988; Moore *et al.* 1988; Crampton and Moore 1990), and terrestrial and marine vertebrates (Keyes 1977; Wiffen 1980, 1981, 1983, 1986; Molnar 1981; Scarlett and Molnar 1984; Wiffen and Moisley 1986; Wiffen and Molnar 1988).

Of special note are some exceptionally well-preserved wood-boring pholadid bivalves. A recent discussion of Antarctic Cretaceous pholadids (Kelly 1988) noted the poorly documented record of these bivalves in the Southern Hemisphere, and the present paper describes the first Cretaceous species known from New Zealand.

The boring bivalves were collected from a single float concretion in Mangahouanga Stream, a tributary of Te Hoe River. Fossiliferous calcareous concretions are concentrated in Mangahouanga Stream, and are derived from fine sandstone of the late Campanian-Maastrichtian Maungataniwha Sandstone which crops out in both banks of the stream. Bored fossil wood is abundant in the concretions, but to date only the single concretion has yielded shells of the bivalves responsible for the borings. The borings themselves have been identified as ichnospecies *Teredolites clavatus* Leymerie (Pl. 3, figs 6–7; see also Kelly and Bromley 1984).

Study of the fauna and sediments in the region of Te Hoe River indicate that the Maungataniwha Sandstone was deposited during a regional marine transgression in a shallow marine nearshore environment on an embayed coastline and in close proximity to a river mouth (Crampton and Moore 1990). Lower Maungataniwha Sandstone includes minor lagoonal sediments, but was deposited mainly on the shoreface or foreshore above fair-weather wave-base. The bulk of this formation was deposited on the lower shoreface to offshore-transition, between fair-weather and storm wave-bases (Crampton and Moore 1990). The stratigraphical position of the fossils described herein is unknown. Fossilized wood occurs as discrete logs and branches which may have borings that enter from all directions, indicating that the wood is probably the same age as the sediment, and was not derived from older, already lithified, lignite beds (see later discussion). The bivalves were collected from araucariacean wood (J. I. Raine, pers. comm. 1989).

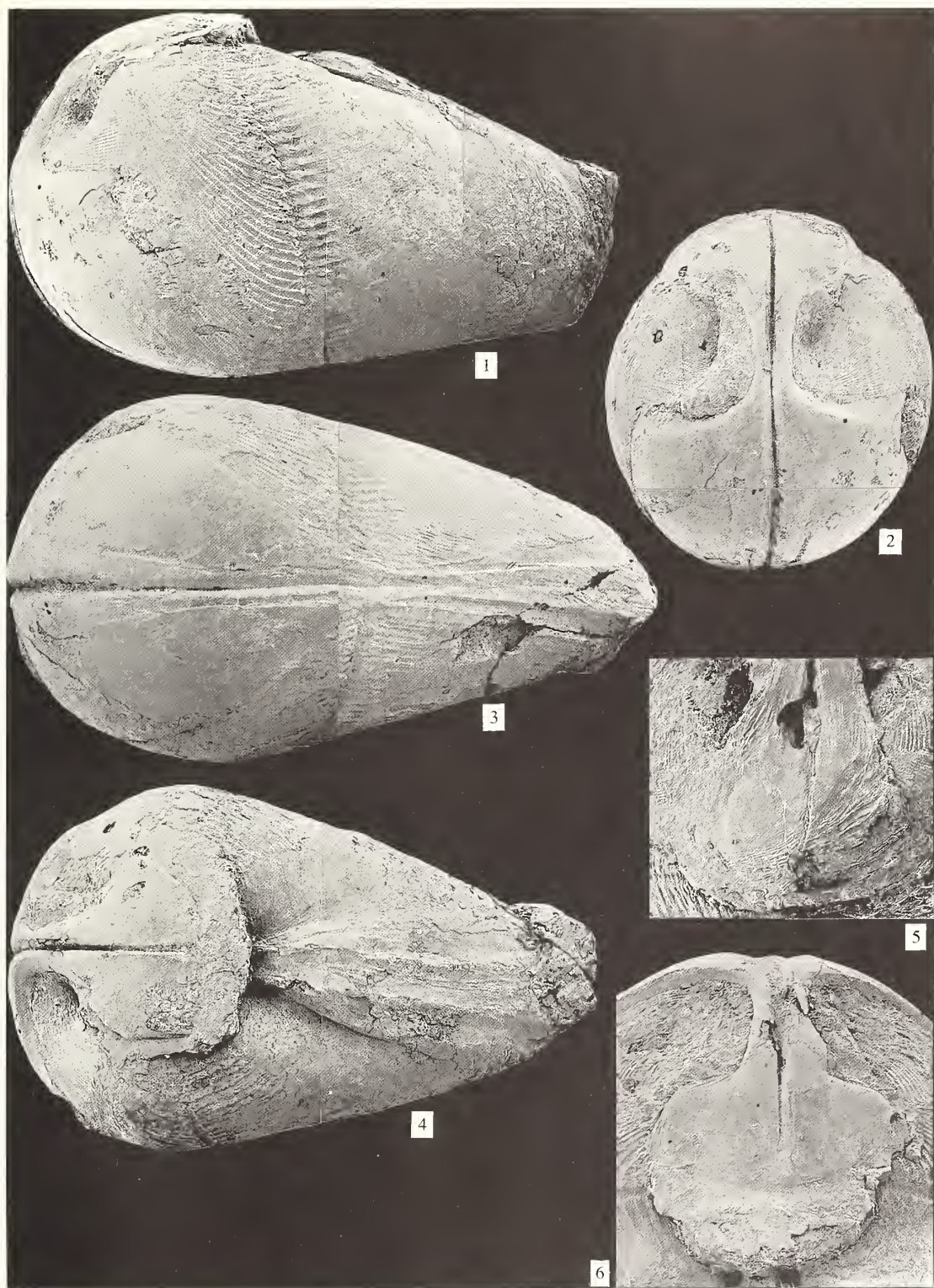
Morphological terminology used in this description follows that of Turner (1969) and Kennedy (1974), as modified by Kelly (1988). Major features of the shell exterior of *Pholadidea* (*Hatasia*)



TEXT-FIG 1. Distribution of Maungataniwha Sandstone (late Campanian-Maastrichtian: shaded) in northwestern Hawkes Bay, New Zealand, showing locality of the fossils described herein (geology after Grindley 1960; Moore 1986; Moore *et al.* 1988).

EXPLANATION OF PLATE 1

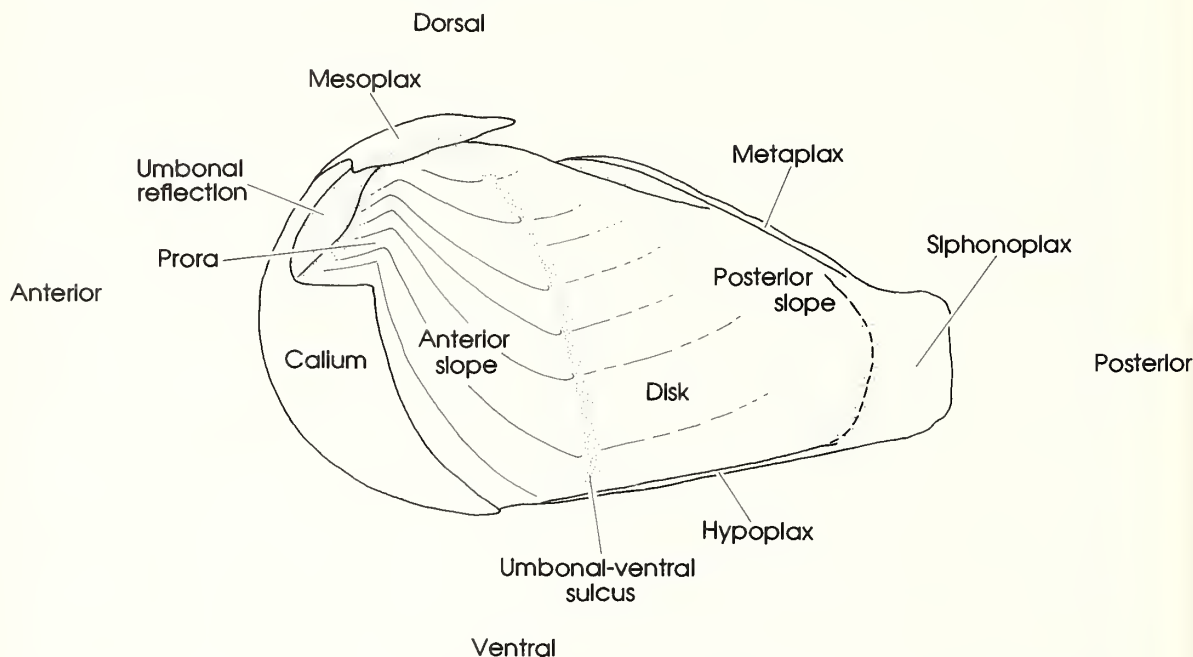
Figs 1-6. *Pholadidea (Hatasia) wiffenae* sp. nov., V19/f6909a, Mangahouanga Stream, northwestern Hawkes Bay, New Zealand (late Campanian-Maastrichtian). All SEM photographs. Note that apparent variations in dimensions are due to orientation of specimen and parallax distortion of the SEM. 1-4, TM 6942 (holotype), adult; 1, lateral aspect, left valve, $\times 5.1$; 2, anterior aspect, valves in occlusion, $\times 4.6$; 3, ventral aspect, valves in occlusion, $\times 5.1$; 4, dorsal aspect, valves in occlusion, $\times 5.1$. 5, TM 6940, mesoplax showing periostracal folds, anterior up, $\times 8.7$. 6, TM 6951, mesoplax, anterior up, $\times 8.2$.



CRAMPTON, *Pholadidea* (*Hatasia*)

wiffenae sp. nov. are illustrated in Text-figure 2. In the following discussion, the bivalves are described as juvenile if the anterior gape is entirely open, immature if the gape is partially closed by callum, and adult if the gape is entirely closed by callum.

Two specimens of the bivalve were transversely serial sectioned (following the recommendation of Kelly 1988) at 500 μm intervals using a Leitz annular saw. These sections were ground to a thickness of 50 μm for examination. In the text individual thin sections are referred to by distance (in millimetres) from the anterior margin of the shell.



TEXT-FIG. 2. External morphology of Martesiinae, after Turner (1969), Kennedy (1974), and Kelly (1988).

SYSTEMATIC PALAEOLOGY

Family PHOLADIDAE Lamarck, 1809

Subfamily MARTESIINAE Grant and Gale, 1931

Genus PHOLADIDEA Turton, 1819

Type species. *Pholadidea loscombiana* Turton, 1819 (original designation).

Subgenus HATASIA Gray, 1851

Type species. *Pholas melanura* Sowerby, 1834 (subsequent designation, Stoliczka 1870).

Discussion. The genus *Pholadidea* is distinguished from other genera in Martesiinae by its single umbonal-ventral sulcus, complete closure of the anterior gape in the adult by a callum which is extended dorsally to cover the beaks, the presence of a mesoplax which is longitudinally divided at some growth stage, and the presence or absence of a metaplax and a hypoplax which, if present, are not separate plates, but result from the deposition of calcite in the periostracum uniting the valves posterior to the umbos (see Turner 1969, p. 716). Two subgenera have been described; *P. (Hatasia)*

is distinguished by a relatively closely appressed umbonal reflection, a comparatively large flat mesoplax in the juvenile overlain dorsally in the adult by a longitudinally divided plate, and a variable siphonoplax composed largely of periostracum (Turner 1969, p. 716). Most *Pholadidea* are shale, soft rock, and coral borers (Turner 1969, see discussion below).

Turner (1969) stated that *Pholadidea* is known from the Eocene-Recent, and the subgenus *P. (Hatasia)* from the Recent only. In his review of Mesozoic pholadids, Kelly (1988) did not list any Cretaceous or older records of *Pholadidea*. Stephenson (1923, 1941) referred a number of Late Cretaceous species from North America to the genus, but his species are known from incomplete specimens or require reinterpretation in the light of the family taxonomy described by Turner (1969). Campbell *et al.* (in press) list *Pholadidea* n. sp., based on well-preserved material, from Palaeocene strata on the Chatham Islands, New Zealand. Re-examination of their material, however, suggests that this species may belong in *Jouannetia* (*Pholadopsis*) Conrad. *P. (H.) wiffenae* sp. nov., therefore, apparently represents the first fossil record for the subgenus, and probably one of the oldest records for the genus.

The genus *Pholadidea* closely resembles both *Martesia* Sowerby and *Opertochasma* Stephenson. *Martesia* are wood-boring pholadids distinguished from *Pholadidea* by an undivided mesoplax, the absence of a dorsal extension of the callum, and by a metaplex and a hypoplex which are separate calcified plates (Turner 1969; Kennedy 1974). Many Cretaceous pholadids formerly assigned to *Martesia* have subsequently been referred to *Opertochasma*, and the earliest confirmed record of *Martesia* is Palaeocene (Speden 1970; Kennedy 1974; Kelly 1988). *Opertochasma* are also wood-borers distinguished by the presence of two umbonal-ventral sulci, periostracal flaps on the posterior slope, and incomplete closure of the anterior gape in the adult (Turner 1969; Speden 1970; Kennedy 1974; Kelly 1988). As noted by Kelly (1988), the second umbonal-ventral sulcus shows considerable intra-population variation in strength, and some specimens may be difficult to distinguish from both *Martesia* and *Pholadidea* (for example, see Speden 1970, pl. 38, figs 2, 4). The first record of *Opertochasma* is in the late Jurassic (Kelly 1988).

Pholadidea (Hatasia) wiffenae sp. nov. is referred to the Martesiinae on the basis of its gross morphology, in particular the complete closure of the anterior gape by a calcareous callum in the adult, and by the absence of protoflex. It is referred to *Pholadidea* because of its dorsally-extended callum, longitudinally divided adult mesoplax, and weakly calcified metaplex and hypoplex within the periostracum uniting valves. The closely appressed umbonal reflection and nature of the mesoplax are consistent with placement in *P. (Hatasia)*.

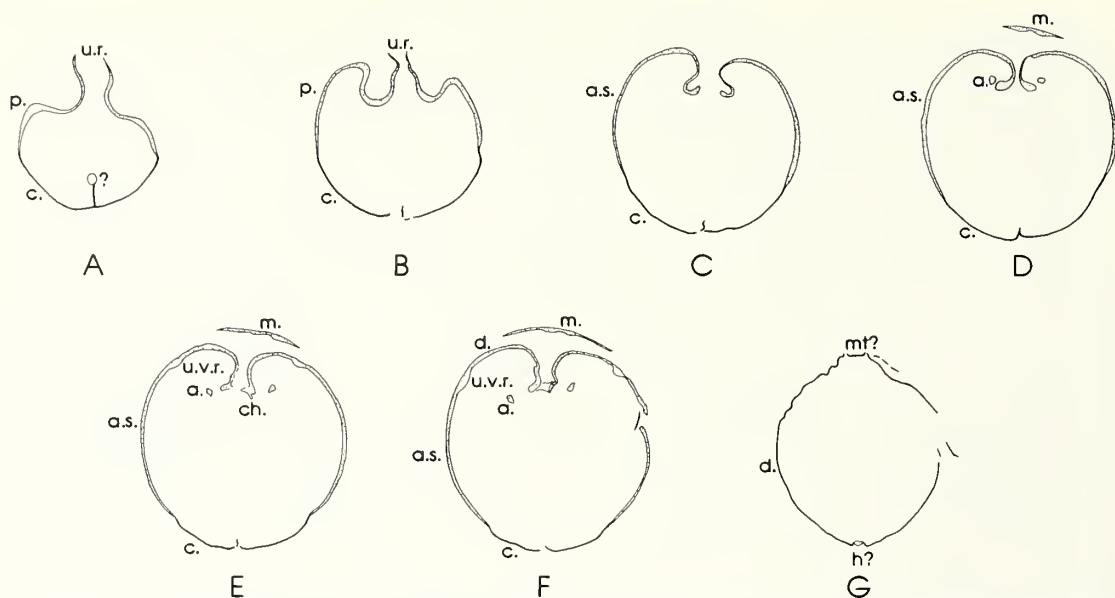
One significant difference between *P. (H.) wiffenae* and typical *Pholadidea* is its wood-boring life-habit. This character, and the well-defined prora (see Turner 1969) suggest affinities with *Martesia*, whereas the life-habit and comparatively narrow commarginal ridges suggest affinities with *Opertochasma*. *P. (H.) wiffenae*, therefore may represent an intermediate between Cretaceous *Opertochasma*, and early Tertiary *Pholadidea* and *Martesia*. It should be stressed, however, that morphological similarities will be the result, in part at least, simply of convergent life habits, which may or may not indicate evolutionary relationships. The influence of substrate type, for example, on shell shape and ornament is outlined in Kennedy (1974). Conclusions about evolutionary relationships, therefore, must await a comprehensive revision of all Cretaceous pholadids, a task hampered by the poor fossil record of this group and the typically incomplete nature of the fossils and early descriptions.

Pholadidea (Hatasia) wiffenae sp. nov.

Plates 1–3; Text-figs 3 and 4

Name. Named after Mrs Joan Wiffen who discovered these bivalves, in recognition of her major contribution to our knowledge of New Zealand late Cretaceous palaeontology.

Type specimens. Holotype: TM 6942, V19/f6909a, GS 14241; entire articulated phosphatized specimen with all accessory plates preserved. Fifteen paratypes: TM 6938–6941, TM 6943–6953, all from V19/f6909a, GS



TEXT-FIG. 3. Interpretive drawings of selected vertical transverse thin sections of *Pholadidea (Hatasia) wiffenae* sp. nov., specimen TM 6953. Sections drawn from photographs, all enlarged $\times 3.4$. Individual drawings oriented dorsal up and arranged with respect to distance from the anterior margin, given below in millimetres. Note that interpretation of sections is hampered by the replacement of originally calcitic shell material by collophane, and the presence of interstitial and cavity-filling collophane. A, 1.5 mm. B, 2.0 mm. C, 2.5 mm. D, 3.0 mm. E, 3.5 mm. F, 4.0 mm. G, 8.0 mm. Legend: a = apophysis; as = anterior slope; c = callum; ch = chondrophore; d = disk; h = hypoplax; m = mesoplax; mt = metaplex; p = prora; ur = umbonal reflection; uvr = umbonal-ventral ridge.

14241. All specimens phosphatized. TM 6952 and TM 6953 serial sections at 0.5 mm intervals through juvenile and adult respectively.

Type locality. Mangahouanga Stream, float concretion 470 m east southeast of Te Hoe forestry road bridge over stream and approximately 200 m downstream from first major true left tributary above bridge, north western Hawkes Bay, New Zealand (see Text-fig 1). New Zealand national Fossil Record locality V19/f6909a, grid reference NZMS 260 sheet V19 42134700. New Zealand Geological Survey collection GS 14241 and Wiffen collection. Collected by J. and M. Wiffen, February 1987.

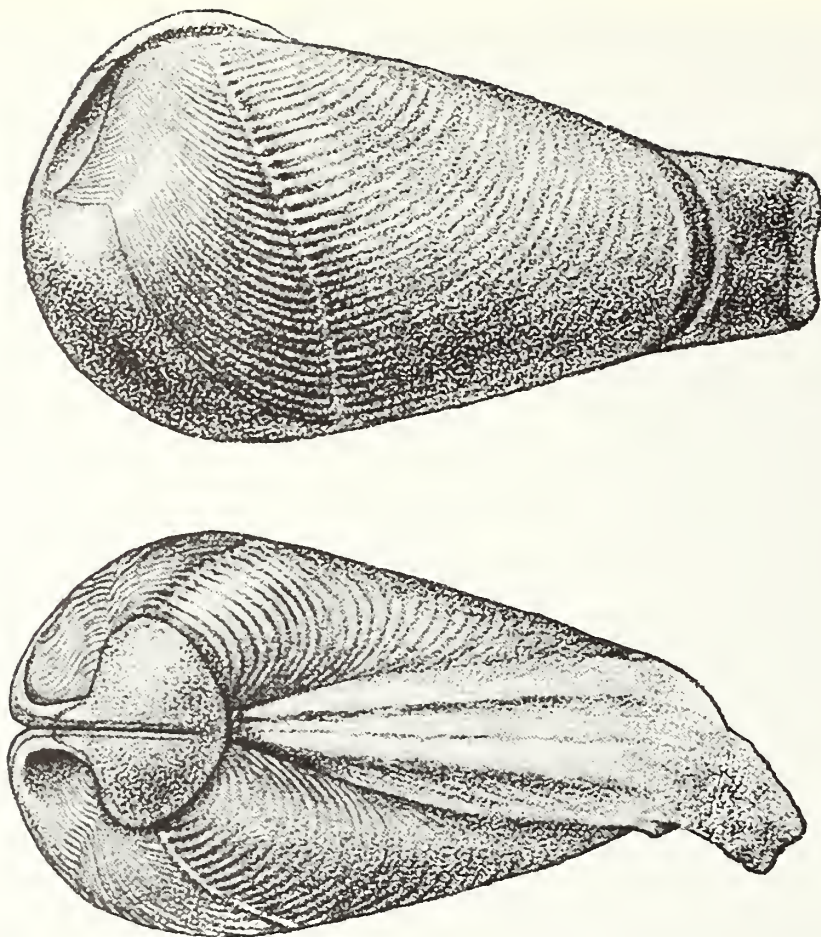
Description. Small, less than 20 mm long, equivalve, inequilateral. Subconical in lateral and vertical profiles, tapering evenly to posterior; subcircular in transverse profile (Pl. 1, figs 1–4; Pl. 2, figs 1–4). Prora well-defined, antero-ventral margin with sharp re-entrant (with sides at approximately 100°) resulting in *Teredo*-like anterior (Pl. 1, fig. 1; Pl. 2, fig. 1; Pl. 3, fig. 1). Posterior-dorsal margin gently convex, posterior margin bluntly rounded, posterior-ventral margin straight to weakly concave. Umbo low, strongly incurved, prosogyrous, at approximately anterior fifth of shell (Pl. 2, fig. 2). Umbonal reflections lower than umbones. Prominent anterior conical cavity beneath umbonal reflection (Pl. 3, figs 1 and 3). Anterior pedal gape confined to ventral

EXPLANATION OF PLATE 2

Figs 1–4. *Pholadidea (Hatasia) wiffenae* sp. nov., V19/f6909a, Mangahouanga Stream, northwestern Hawkes Bay, New Zealand (Campanian-Maastrichtian). All SEM photographs. Note that apparent variations in dimensions are due to orientation of specimens and parallax distortion of the SEM. 1 and 3, TM 6941, adult; 1, lateral aspect, left valve, $\times 4.9$; 3, dorsal aspect, valves in occlusion, $\times 4.9$. 2 and 4, TM 6938, immature; 2, dorsal aspect, mesoplax removed, valves in occlusion, $\times 5.1$; 4, ventral aspect, $\times 5.1$.



CRAMPTON, *Pholadidea (Hatasia)*

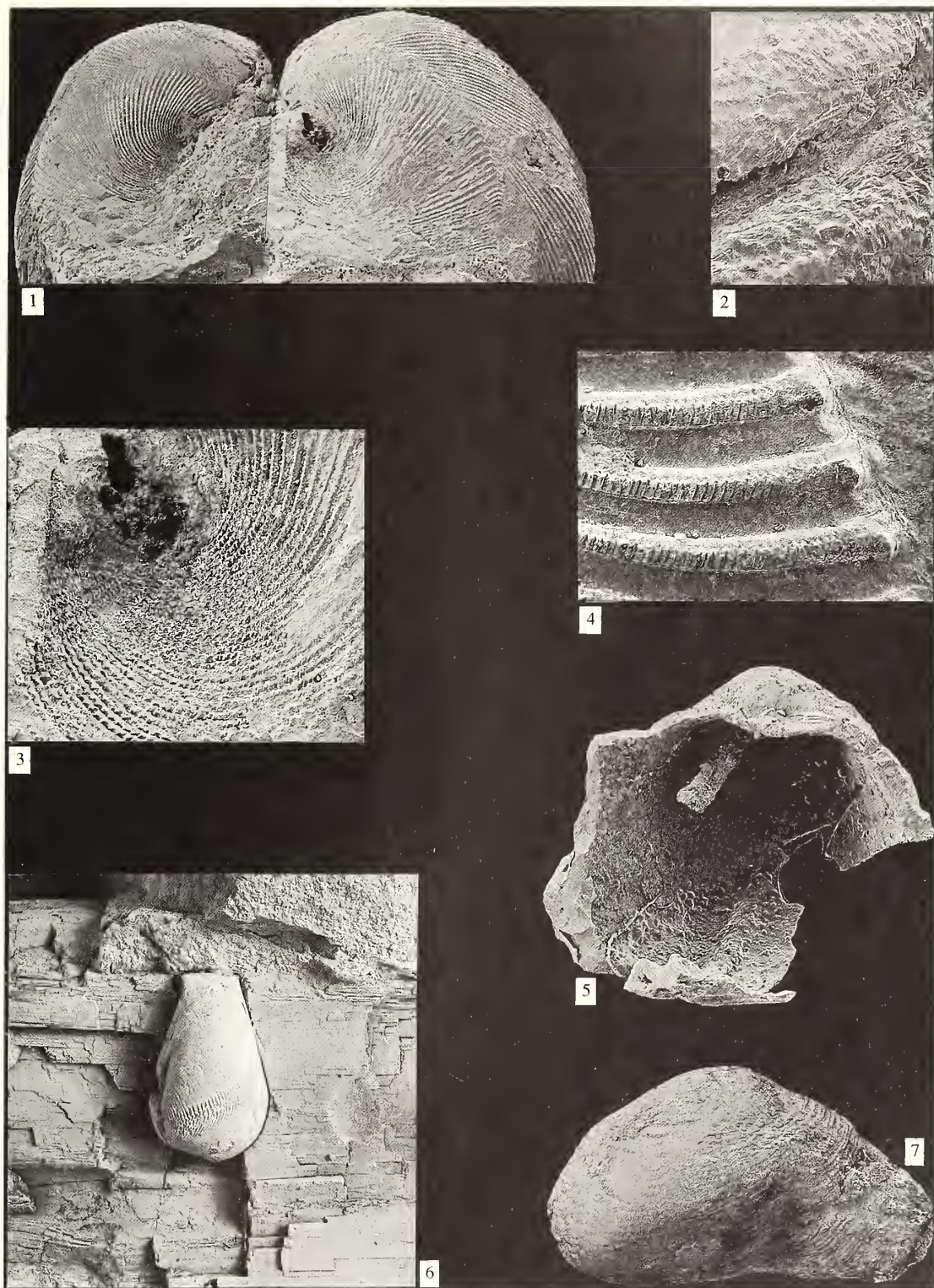


TEXT-FIG. 4. Reconstruction of *Pholadidea (Hatasia) wiffenae* sp. nov. Note that juvenile mesoplax (omitted here) may underlie longitudinally divided adult mesoplax shown, and may extend posteriorly well beyond adult mesoplax (see discussion in text). (Drawn by R. C. Brazier.)

half of height, subtriangular, dorsal margin of gape concave, almost perpendicular to commissure. Anterior gape entirely closed in adults by a callum, the two halves of which are inferred to have been connected by periostracum medially, are slightly raised above level of anterior slope, and extend dorsally over the umbonal reflection (Pl. 1, figs 2 and 3). A few prominent commarginal growth lines present on callum of all specimens examined. Protostracum lacking. Mesoplax of two pear-shaped plates which cover umbones and become fused

EXPLANATION OF PLATE 3

Figs 1–7. *Pholadidea (Hatasia) wiffenae* sp. nov., V10/f6909a, Mangahouanga Stream, northwestern Hawkes Bay, New Zealand (Campanian-Maastrichtian). All SEM images except Fig. 6. 1 and 3, TM 6950, juvenile, anterior aspect of prora and umbonal reflection, dorsal up; 1, $\times 10.5$; 3, $\times 34.7$. 2, TM 6940, detail of callum at commissure, showing texture resulting from incorporation of clastic grains into periostracum, $\times 22.4$. 4, TM 6941, denticulate ornament on anterior slope immediately adjacent to umbonal-ventral sulcus, dorsal up, anterior to left, $\times 41.6$. 5, TM 6949, interior of juvenile, showing apophysis and umbonal-ventral ridge, anterior to right, $\times 19.1$. 6, TM 6942 (holotype) in life position in araucariacean wood, $\times 1.7$. 7, TM 6954, ichnospecies *Teredolites clavatus* Leymerie, resulting from boring by *Pholadidea (Hatasia) wiffenae* sp. nov., aperture to right, $\times 3.6$.



posteriorly (Pl. 1, figs 2, 4–6; Pl. 2, fig. 3). Mesoplax closely associated with, and possibly partially fused to, dorsal projections of the callum. The juvenile portion of the mesoplax characteristic of subgenus *Hatasia* (see above), is not clearly visible on any specimens, but may be represented by the flow flange surrounding and possibly underlying the longitudinally divided portion of the mesoplax (Pl. 1, figs 4–6). In thin section, specimen TM 6953, interpreted as an adult on the basis of its complete callum, displays a single large flat plate which extends 3.0–4.0 mm behind the umbo, and which is interpreted as the juvenile mesoplax (Text-fig. 3). This specimen apparently lacks the divided mesoplax observed on other individuals. Metaplex and hypoplex comprising anteriorly tapering, partially calcified periostracum, uniting valves across dorsal and ventral gapes respectively (Pl. 1, figs 3 and 4; Pl. 2, figs 2–4). Umbonal-ventral sulcus well-defined, narrow. Matched on shell interior by narrow upstanding umbonal-ventral ridge (Pl. 3, fig. 5; Text-fig. 3). Sculpture on prora and anterior slope of between 50 and 70 sharply-defined, narrow, rounded commarginal ridges and broader, flat-floored troughs. Ridges finely denticulate on anterior slope (Pl. 3, fig. 4). Ridges broader and weaker on disc, fading out over posterior slope of many specimens. Periostracum present over entire shell, thicker on disc and posterior slope than elsewhere. In some specimens clastic grains incorporated into periostracum over callum (Pl. 3, fig. 2) and, more commonly, over posterior slope. Siphonoplex short, composed of periostracum or partly calcified periostracum (Pl. 2, fig. 1; Pl. 3, fig. 6). Apophysis relatively short, rod-like, not markedly spatulate at distal end (Pl. 3, fig. 5; Text-fig. 3).

Dimensions (undistorted specimens, mm).

Specimen	Length (excluding siphonoplex)	Height	Width (both valves)
TM 6938 (immature)	17.6	10.8	11.0
TM 6941 (adult)	17.1	9.7	10.4
TM 6942 (adult, holotype)	17.6	11.3	11.3
TM 6943 (adult)	17.2+	10.7	10.6
TM 6944 (adult)	?	8.9	8.8
TM 6945 (?)	?	c. 11.0	11.1
TM 6946 (adult)	15.5	9.0	8.9
TM 6947 (juvenile)	14.7+	9.8	9.7
TM 6948 (adult)	18.9	10.1	11.0
TM 6953 (adult)	c. 12.6	8.1	c. 8.0

Discussion. A number of late Cretaceous pholadids have been described from the Southern Hemisphere, but incomplete knowledge of these, in most cases, prevents detailed comparison with the present species. *Martesia leali* Stinnesbeck, 1986 (pp. 185–186, pl. 5, fig. 9) from the Maastrichtian of Chile, resembles *P. (H.) wiffenae* in gross form and life habit, but possesses a coarser ornament (although, as mentioned above, the nature of the substrate can have a marked effect on ornament, see Kennedy 1974). The nature of the accessory plates in *M. leali* is unknown. *Martesia cazadoriana* Wilckens, 1907 (pp. 10–11, pl. 8, fig. 11), from the Campanian-Maastrichtian (Riccardi 1988) of Patagonia, is known only from a single internal mould; and *Martesia?* sp. of Rennie (1930, pp. 205–206, pl. 23, figs 13 and 14) from the late Cretaceous of South Africa, is known from a single incomplete and distorted specimen, and probably does not belong in *Martesiinae* (Kelly 1988). Many late Cretaceous pholadids have been described from the Northern Hemisphere, and although superficially some of these resemble *P. (H.) wiffenae*, detailed comparisons should be made within the framework of a comprehensive systematic review of the family.

Acknowledgements. I would like to thank Joan and Pont Wiffen who found and extracted these bivalves, and donated them to the NZ Geological Survey. Skilled technical assistance was given by J. Simes (SEM photography), W. St George (light photography), N. Orr (thin sectioning), R. C. Brazier (drawings), and S. Nepe (typing). Earlier drafts of this paper were reviewed and greatly improved by Drs J. G. Begg (New Zealand Geological Survey, Lower Hutt), S. R. A. Kelly (British Antarctic Survey, Cambridge), P. A. Maxwell (New Zealand Geological Survey, Lower Hutt), N. J. Morris (British Museum of Natural History), and R. D. Turner (Museum of Comparative Zoology, Harvard University).

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Typescript received 18 September 1989

Revised typescript received 4 January 1990

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Fig. 1. *Ammonia beccarii* (Linné). Repository and catalogue number, description, locality, horizon, magnification.

Figs 2–6. *Ephidium crispum* (Linné). 2, repository and catalogue number, description, locality, horizon, magnification. 3, repository, etc. 4, etc. 5, etc. 6, etc.

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Authors are encouraged to use symbols to indicate the degree of confidence with which synonymy entries are referred to the species under discussion. Such symbols are given in MATTHEWS, S.C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, **16**, 713–719. It may also be useful to consult BENGSTON, P. 1988. Open nomenclature. *Palaeontology*, **31**, 223–227. Additional information at the end of synonymy entries is enclosed in square brackets.

The recommended style is:

Order PHACOPIIDA Salter, 1864
Suborder CHEIRURINA Harrington and Leanza, 1957
Family ENCRINURIDAE Angelin, 1854
Subfamily ENCRINURINAE Angelin, 1854
Genus ENCRINURUS Emmrich, 1844

Type species. *Entomostracites punctatus* Wahlenberg, 1818 from the Wenlock of Gotland, Sweden.

Subgenus ENCRINURUS (ENCRINURUS) Emmrich, 1844

Type species. As for genus.

Encrinurus (*Encrinurus*) *macrourus* Schmidt, 1859

Plate 41, figs 1–10; Plate 42, figs 1–11; Text-fig. 5

- *1859 *Encrinurus punctatus* var. *macrourus* Schmidt, p. 438.
- .1941 *Encrinurus punctatus* (Wahlenberg) 1821 [sic]; Rosenstein, text-fig. 4A, pl. 2, fig. 4–4b.
- v.1962 *Encrinurus macrourus* Schmidt; Tripp [partim], p. 469, pl. 65, figs 1, 3, 4; pl. 66, fig. 1a–c; pl. 67, figs 2–4; pl. 68, figs 1, 3, ?9; non pl. 65, fig. 2 [= *E. (E.) punctatus*]; pl. 67, fig. 1; pl. 68, fig. 2 [= *E. (E.)* cf. *intersitus* sp. nov.].
- .1972 *Encrinurus (E.)* cf. *punctatus* 2; Schrank [partim], p. 38, pl. 11, fig. 4 [figs 1, 2, 7 = paratypes of *E. (E.) ruhneensis* Männil, 1978; figs 3, 5, 6 indeterminate].
- non 1972 *Encrinurus (E.)* cf. *punctatus macrourus* Schmidt, 1859; Schrank, p. 42, pl. 12, fig. 6 [? = *E. (E.) ruhneensis* Männil, 1978], fig. 7 [? = *E. (E.) punctatus*].

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Examples:

- BOUCOT, A. J. 1981. *Principles of benthic marine paleoecology*. Academic Press, New York and London, xv+463 pp.
- and JOHNSON, I. G. 1979. Pentamerinae (Silurian brachiopods). *Palaeontographica, Abteilung A*, **163**, 87–129.
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- . 1934b. Downtonian Merostomata from Spitzbergen, with remarks on the suborder Synziphosura. *Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo. I. Matematisk-Naturvidenskapelig Klasse*, **1934** (3), 1–26.
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1



2



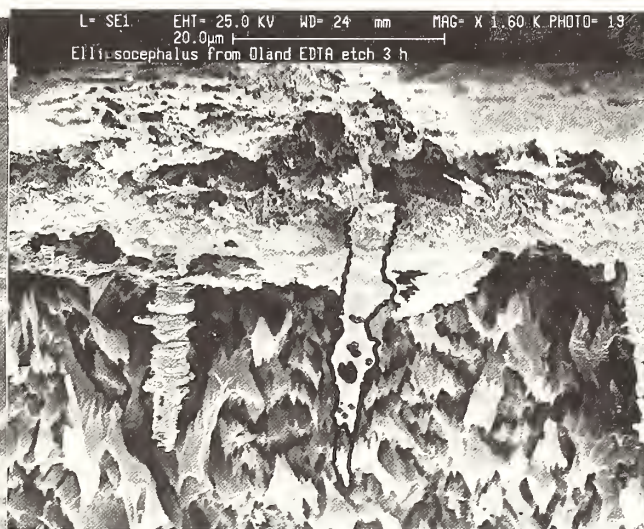
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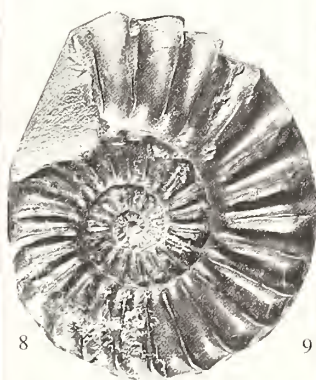
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- iv, Prefatory text, which should contain the abstract from the parent paper, should be included.
- v, All pages must be consecutively numbered.

Authors with large sections for deposition are advised to consult the Secretary of the Publications Committee for further information.

SPECIAL PAPERS IN PALAEOONTOLOGY

Preparation of papers for this series should be in the same style as for *Palaeontology*.

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Cost of publication. The Association's funds for this series are limited. Authors are asked to obtain grants wherever possible. Scripts should not normally exceed the equivalent of 110 published pages.

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GRANTS IN AID OF PUBLICATION

Palaeontology has no compulsory page or plate charges. However, authors are requested to seek grants in aid of publication from their institutions or from research funds, or to apply for publication costs in research grants. Such financial support is particularly welcome, and may be essential, for long papers.

Although acceptance of a paper for publication will not depend on the receipt of such grants, authors will appreciate that the funds available to the Association for publication are limited. Every grant or donation will therefore directly help the Association's publication programme.

THE PALAEOONTOLOGICAL ASSOCIATION

ANNUAL REPORT OF COUNCIL FOR 1989

MEMBERSHIP AND SUBSCRIPTIONS. Membership totalled 1,285 on 31 December 1989, an increase of 10 over the previous year. There were 808 Ordinary Members, an increase of 4; 83 Retired Members, an increase of 10; 113 Student Members, an increase of 4, and 281 Institutional Members, a decrease of 8. Total individual and institutional subscriptions to *Palaeontology* through Basil Blackwell's agency numbered 438, an increase of 2.

Subscriptions to *Special Papers in Palaeontology* numbered 100 individuals, a decrease of 9, and 114 Institutions, a decrease of 3. Orders through Basil Blackwell's agency for *Special Papers* totalled 108 volumes.

Sales of backparts of *Palaeontology* via the Membership Treasurer realized £370.05. Sales of back numbers of *Special Papers in Palaeontology* to individuals yielded £771.50, and to Institutions £219.00.

Almost all sales of the *Field Guides to Fossils* series resulted from the activities of the Marketing Manager, *Fossils of the Chalk* yielding £2,381, *Fossil Plants of the London Clay*, £413 and *Zechstein Reef Fossils and their Palaeoecology*, £587. The *Atlas of Invertebrate Macrofossils* yielded £959 (£870 of which was royalties from sales), the *Burgess Shale Portfolio* yielded £88 and sales of the *Malta Field Guide*, £2.50.

FINANCE. During 1989 the Association published Volume 32 of *Palaeontology* at an estimated cost of £72,208 (including postage and distribution). *Special Papers 41* and *42* were published at an estimated cost of £4,600 and £9,300 respectively (including postage and distribution). The Association is grateful to all those who made donations to offset the cost of publishing *Palaeontology* and *Special Papers*.

PUBLICATIONS. Volume 32 of *Palaeontology*, published in 4 parts during 1989, contained 917 pages and 107 plates. *Special Papers 41* and *42* were published. Due to the sudden closure of the Oxford University Press Printing House, the Association had to appoint new printers; Cambridge University Press were chosen and Parts 2–4 of *Palaeontology* were printed there.

MEETINGS. Nine meetings were held in 1989. The Association is indebted to the organizers, hosts and field leaders of these.

- a. *Review Seminar* on 'The Cretaceous/Tertiary Boundary' held on 15 February at the University Museum, Oxford and convened by Dr R. A. Spicer.
- b. *Lyell Meeting* held jointly with the Geological Society, on 'Palaeoclimates' on 22 February at Burlington House and convened by Dr C. P. Summerhayes.
- c. *Thirty-second Annual General Meeting* held in the Department of Geology, Imperial College on 15 March. Dr Dianne Edwards delivered the Annual Address on 'Pioneering plants'. The Sylvester-Bradley Award was made to Patrick Wyse Jackson.
- d. *Field Meeting* to Yorkshire Jurassic plant localities, led by Dr C. R. Hill on 7–9 April. 21 people participated.
- e. *Progressive Palaeontology* meeting, an open meeting for presentations by research students was held at University of Wales College of Cardiff on 17 May. It was convened by Andrew King.
- f. *Seminar and Workshop* on 'Physical Modelling in Palaeontology' was held at the Department of Earth Sciences, Cambridge on 9 October. It was convened by Sue Rigby and Clare Milsom.
- g. *Joint One Day Meeting* with the Malacological Society on 'The functional morphology of the mollusc shell', held on 25 October in the British Museum (Natural History). The meeting was convened by Dr J. D. Taylor and Dr J. A. Crame. Approximately 75 people attended.
- h. *Review Seminar* on 'Macroevolution' held at the Open University on 15 November and convened by Dr P. W. Skelton. Over 180 people attended.
- i. *Review Seminar* held jointly with the Geological Society, on 'Carbonate buildups' on 30 November at Derbyshire College of Higher Education. The convenor was Dr P. Bridges and there were 80 participants.
- j. *The Annual Conference*, held at the University of Liverpool on 18–21 December was an open meeting, with a thematic session on 'Functional Morphology'. The Local Secretary was Dr C. R. C. Paul and the meeting was attended by about 150 people.

COUNCIL. The following members served on Council following the Annual General Meeting on 15 March 1989. *President*, Dr J. D. Hudson; *Vice-Presidents*, Dr P. W. Skelton, Dr M. Romano; *Treasurer*, Dr M. E. Collinson; *Secretary*, Dr P. Wallace; *Membership Secretary*, Dr H. A. Armstrong; *Institutional Membership Treasurer*, Dr A. W. Owen; *Editors*, Dr M. J. Benton (also Public Relations Officer), Dr J. E. Dalingwater, Dr D. Edwards, Dr C. R. C. Paul, Dr P. A. Selden, Dr P. D. Taylor; *Marketing Manager*, Dr C. R. Hill; *Circular Reporter*, Dr D. Palmer; *Other Members*, Dr J. A. Crame, Dr G. B. Curry, Dr E. A. Jarzembowski, Dr R. A. Spicer. Dr D. M. Martill was co-opted in 1989.

COUNCIL ACTIVITIES. In conjunction with other Societies, Council lobbied the Post Office to issue a set of commemorative stamps in 1991 to mark the 150th anniversary of the first use of the term 'dinosaur' by Sir Richard Owen. The suggestion was accepted and four postage stamps bearing pictures of four British dinosaurs representing four major types of dinosaur will be issued in 1991.

Many amateur palaeontologists make highly significant and often entirely altruistic contributions to palaeontology, ranging from the making of collections to their study, care and conservation. Council has decided to recognize this contribution by an Award for Amateur Palaeontologists: the first award will be made to Mr Alan Dawn at the AGM in March 1990.

The new A5 format *Palaeontology Newsletter* continues to be published, although problems with printers made it necessary to combine issues 3 and 4 in one volume. It is attracting favourable comment and varied contributions are beginning to be submitted.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1989

BALANCE SHEET AS AT 31 DECEMBER 1989

1988			
£	£		£
52,359		INVESTMENTS AT COST (see schedule)	55,691
		CURRENT ASSETS	
6,596		Sundry Debtors	3,213
28,966		Cash at bank	56,706
2,476		Sylvester-Bradley Fund	2,587
450		Loans	450
6,811		Stocks at valuation	4,525
45,299			67,481
		CURRENT LIABILITIES	
3,060		Subscriptions received in advance	3,752
		Provision for cost of:	
—		<i>Palaeontology</i>	16,000
—		<i>Special Papers</i>	13,900
7,880		Sundry creditors	1,305
10,940			34,957
34,359			32,524
86,718			88,215
		Represented by:	
		PUBLICATIONS RESERVE ACCOUNT	
99,726		Balance brought forward	83,025
(16,701)		Excess of income over expenditure for the year transferred from from Income and Expenditure Account (1988) deficit	1,386
83,025			84,411
		SYLVESTER-BRADLEY FUND	
1,885		Balance brought forward	2,476
86		Interest	169
(200)		Grant awarded	(200)
705		Donations	142
2,476			2,587
1,217		MEETING RESERVE	1,217
86,718			88,215

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31 DECEMBER 1989

INCOME

1988			£	£
£				
	SUBSCRIPTIONS			
	1989		38,663	
	1988		717	
39,833				39,380
	<i>PALAEONTOLOGY</i>			
	Sales		34,024	
	Donations		518	
34,226				34,542
	<i>SPECIAL PAPERS</i>			
	Sales		5,558	
	Donations		2,000	
11,292				7,558
	BURGESS SHALE PORTFOLIO			
53	Sales			88
	<i>FOSSIL PLANTS OF THE LONDON CLAY</i>			
951	Sales			413
	<i>FOSSILS OF THE CHALK</i>			
6,340	Sales			2,427
	<i>ZECHSTEIN REEF FOSSILS</i>			
82	Sales			587
	<i>ATLAS OF INVERTEBRATE MACROFOSSILS</i>			
811	Sales			959
	<i>PALSTAT</i>			
	Income		—	
	Expenses		—	
82				—
(201)	OFFPRINTS			1,178
—	PROFIT ON SALES OF INVESTMENTS			3,454
10,153	INVESTMENT INCOME (see schedule)			11,297
54	SUNDRY INCOME			3
£103,676				£101,886

EXPENDITURE

1988 £		£	£
	COST OF PUBLICATION OF <i>PALAEONTOLOGY</i>		
	Volume 32 – Part 1	18,272	
	Part 2	18,336	
	Part 3	14,316	
	Part 4 (prov.)	16,000	
	Paper purchased from OUP	5,284	
82,420			72,208
	COST OF PUBLICATION OF <i>SPECIAL PAPERS</i>		
	No. 41 (prov.)	4,600	
	No. 42 (prov.)	9,300	
18,038			13,900
	<i>FOSSILS OF THE CHALK</i>		
	Cost of books sold	1,889	
5,029			1,889
	<i>ZECHSTEIN REEF FOSSILS</i>		
	Cost of books sold	397	
1,366			397
—	COST OF SCIENTIFIC MEETINGS		579
—	ADVERTISING FIELD GUIDES SERIES		449
2,499	WAREHOUSING OF PUBLICATIONS		(3,193)
250	GRANTS		50
	COST OF NEWSLETTERS		
	Preparation	4,860	
	Postage	3,259	
	Credit	(1,125)	
3,867			6,994
	ADMINISTRATIVE COSTS		
	Postage, stationery, telephone	3,150	
	Editorial expenses	965	
	Meeting expenses	2,155	
	Audit fee	275	
	Stockbroker fee	564	
	Membership of Societies	118	
6,908			7,227
£120,377			£100,500
	EXCESS OF INCOME OVER EXPENDITURE FOR THE YEAR TRANSFERRED TO PUBLICATIONS RESERVE ACCOUNT (1988 deficit)		£1,386

SCHEDULE OF INVESTMENTS AND INVESTMENT INCOME AS AT 31 DECEMBER 1989

		Cost £	Gross Income for Year £
£2,000	11 % Exchequer Stock 1991	1,991	220
£1,000	9 % Treasury Stock 1992/96	992	90
£10,000	9 % Treasury Stock 1994	9,943	900
£4,000	8 % Treasury Stock 2002/6	2,192	320
£5,357	13 $\frac{1}{4}$ % Treasury Stock 1997	5,000	710
£3,280	13 $\frac{1}{4}$ % Exchequer Stock 1996	3,000	434
5,270	M & G Charifund Units	4,073	1,945
1,872	M.E.P.C. p.l.c. 25p shares	4,939	177
2,280	National Westminster Bank p.l.c. £1 Ordinary Shares	3,929	451
10,150	Agricultural Mortgage Corporation Ltd. 7 $\frac{3}{4}$ % Debenture Stock 1991/93	8,251	786
10,000	New Throgmorton Trust (1983) p.l.c. 25p Income Shares	1,706	739
1,460	Saatchi & Saatchi 6.3 % Convertible Cumulative Redeemable Preference £1 Shares	1,994	123
£2,100	Hanson Trust p.l.c. 10 % Convertible Unsecured Loan Stock 2007/12	2,974	210
£4000	Cable & Wireless 7 % convertible unsecured loan stock 2008	4707	140
			7,369
	Bank Interest		3,924
		55,691	11,297
	MARKET VALUE at 31 December 1989 (1988-£91,931)	£103,579	

REPORT OF THE AUDITOR TO THE MEMBERS OF
THE PALAEOONTOLOGICAL ASSOCIATION

In my opinion, the Accounts as set out above give a true and fair view of the state of the affairs of the Association at 31 December 1989 and of its income and expenditure for the year ended on that date.

March 1990
Market Harborough, Leicestershire

G. R. POWELL
Chartered Accountant

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VOLUME 33

Palaeontology

1990

PUBLISHED BY THE
PALAEOLOGICAL ASSOCIATION
LONDON

Dates of Publication of Parts of Volume 33

Part 1, pp. 1–256	21 March 1990
Part 2, pp. 257–502	31 May 1990
Part 3, pp. 503–748	7 August 1990
Part 4, pp. 749–1000	16 November 1990

THIS VOLUME EDITED BY M. J. BENTON, J. E. DALINGWATER, D. EDWARDS,
P. D. LANE, C. R. C. PAUL, P. A. SELDEN AND P. D. TAYLOR

Date of Publication of Special Paper in Palaeontology

Special Paper No. 43, 5 April 1990

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*Printed in Great Britain
by Cambridge University Press*

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